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NOVA ABORDAGEM METODOLÓGICA DE MODELAGEM COMPUTACIONAL E DETERMINAÇÃO DE ÁREAS PRIORITÁRIAS PARA PROSPECÇÃO DE FÓSSEIS DA MEGAFAUNA QUATERNÁRIA

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DISSERTAÇÃO DE MESTRADO

Programa de Pós-Graduação em Geociências e Análise de Bacias

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por:

Wilcilene Santos de Aragão
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DISSERTAÇÃO DE MESTRADO

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Resumo

As descobertas fósseis da megafauna quaternária em Sergipe tiveram início em 1884, com ocorrência predominantemente em afloramentos do tipo tanque. Atualmente há registros de ocorrências de herbívoros das espécies *Catonyx cuvieri*, *Equus neogeus*, *Eremotherium laurillardi*, *Notiomastodon platensis*, *Pachyarmatherium brasiliense*, *Paleolama major*, *Toxodon platensis*, além de registros indeterminados de *Glyptotherium* e *Mylodontidae*. No grupo dos carnívoros, a única espécie com ocorrência para o estado é *Smilodon populator*. Modelos de paleodistribuição podem auxiliar na identificação de regiões com maiores chances de ocorrência pretérita das espécies e a combinação de projeções desses modelos com algoritmos de priorização de áreas como o *Zonation*, pode constituir um *framework* metodológico aplicável à prospecção fóssil. O objetivo deste trabalho é determinar regiões com maior potencial fossilífero em Sergipe, através do uso de dados de paleodistribuição das espécies, vieses tafonômicos, informações geomorfológicas e uso dos espaços geográficos adicionados ao *software Zonation,* e comparar com o que é conhecido na literatura para o Estado. A construção dos modelos de paleodistribuição foi realizada utilizando o Maxent, algoritmo que combina registros de ocorrências com dados climáticos especializados para a confecção de mapas de adequabilidade climáticas. A validação desses mapas foi feita através da análise dos valores da métrica AUC (AUC - *Area Under the ROC Curve*). Na etapa de determinação de áreas prioritárias foi utilizado o *Zonation*, que combina os mapas de adequabilidade gerados com dados espaciais de registros de cavernas, variação da elevação e densidade rural do Brasil. As 14 espécies estudadas apresentaram modelos com boa performance preditiva (AUC > 0,75) possibilitando o uso dos mapas obtidos no *Zonation*. Como resultado, obtivemos um mapa único com as áreas de maior probabilidade de ocorrência fossilífera para todo o conjunto de espécies analisadas. Utilizando o estado de Sergipe como referência, as áreas mapeadas com alta prioridade fossilífera para o estado corroboram com as regiões já conhecidas com ocorrência fossilífera e que estão disponíveis na literatura. Outras áreas onde ainda não se conhece ocorrência de fósseis se mostraram potencialmente fossilíferas, podendo ser alvo de futuros esforços de prospecção, inclusive como forma de validação para o modelo apresentado. Diante dos resultados positivos obtidos, pode-se considerar que essa metodologia é válida para outros estudos que tiverem o mesmo objetivo, podendo servir como um arcabouço metodológico consistente para o mapeamento de áreas de priorização para prospecção fóssil. Futuros estudos empíricos serão importantes para refinar os resultados da metodologia proposta, bem como possibilitar uma validação mais abrangente da mesma.

Palavras-chave: *Maxent.* Modelagem de nicho. Potencial fossilífero. *Zonation*

Abstract

The fossil discoveries of the quaternary megafauna in Sergipe began in 1884, occurring predominantly in outcrops of the tank type. Currently there are records of occurrences of herbivores of the species *Catonyx cuvieri*, *Equus neogeus*, *Eremotherium laurillardi*, *Notiomastodon platensis*, *Pachyarmatherium brasiliense*, *Paleolama major*, *Toxodon platensis*, in addition to indeterminate records of *Glyptotherium* and *Mylodontidae*. In the group of carnivores, the only species with occurrence for the state is *Smilodon populator*. Paleodistribution models can assist in the identification of regions with greater chances of past species occurrence and the combination of projections of these models with algorithms for prioritizing areas such as *Zonation*, can constitute a methodological framework applicable to fossil prospecting. The objective of this work is to determine regions with greater fossiliferous potential in Sergipe, through the use of species paleodistribution data, taphonomic biases, geomorphological information and use of the geographical spaces added to the *Zonation* software, and to compare with what is known in the literature for the State. The construction of paleodistribution models was performed using Maxent, an algorithm that combines occurrence records with spatialized climatic data for the preparation of climate suitability maps. The validation of these maps was done by analyzing the values of the AUC (AUC - *Area Under the* ROC *Curve*) metric. In the step of determining priority areas, Zonation was used, which combines the generated suitability maps with spatial data from cave records, elevation variation and rural density in Brazil. The 14 species studied presented models with good predictive performance (AUC> 0.75) enabling the use of maps obtained in Zonation. As a result, we obtained a single map with the areas most likely to occur fossiliferous for the entire set of species analyzed. Using the state of Sergipe as a reference, the areas mapped with high fossiliferous priority for the state corroborate the regions already known to have fossiliferous occurrences and which are available in the literature. Other areas where the occurrence of fossils is still unknown are potentially fossiliferous, and may be the target of future prospecting efforts, including as a means of validating the model presented. In view of the positive results obtained, it can be considered that this methodology is valid for other studies that have the same objective, and can serve as a consistent methodological framework for mapping priority areas for fossil prospecting. Future empirical studies will be important to refine the results of the proposed methodology, as well as to enable a more comprehensive validation of it.

Keywords: *Maxent*. Niche modeling. Fossiliferous potential. *Zonation*

SUMÁRIO

CAPÍTULO 1 – INTRODUÇÃO

1.1 - Apresentação

Os padrões de distribuição de espécies podem sofrer mudanças com o tempo, sendo capaz de expandir-se, retrair-se ou deslocar-se de acordo com as variações ambientais, suas características ecológicas e suas interações com outras espécies. Uma das formas para determinar o potencial de distribuição de uma espécie é inferir o espaço geográfico que contém condições ambientais onde sabe-se que a espécie ocorreu e que, portanto, podem ser consideradas adequadas para o estabelecimento de suas populações. Atualmente, esse potencial de distribuição é inferido através da modelagem de distribuição de espécies (SDM - *Species distribution modeling*) e são utilizadas na Paleontologia em conjunto com modelos paleoclimáticos para projetar distribuições de espécie de animais e plantas do passado, conhecidas como paleodistribuição ou paleo-SDM (Jakob *et al*., 2009; Varela *et al*., 2010; Franklin *et al*., 2015).

As projeções de paleodistribuição têm sido preferencialmente utilizadas na indicação de potenciais áreas de distribuição de espécies extintas do Quaternário (Varela *et al*., 2010; Lima-Ribeiro *et al*., 2012; Varela *et al*., 2018). As alterações em suas áreas de distribuição potencial são avaliadas especialmente em momentos climáticos críticos, como o último máximo glacial há ~ 21 mil anos (ka) e o ótimo climático do Holoceno (~ 6 ka) (Svenning *et al*., 2011; Lima-Ribeiro *et al*., 2012; Maguire *et al*., 2015; Varela e Fariña, 2015; Varela *et al*., 2018). Um uso menos recorrente é a aplicação da paleodistribuição para auxiliar a identificação taxonômica de fósseis incompletos (França *et al*., 2014; Eduardo *et al*., 2018).

Até o momento, modelos de paleodistribuição têm sido pouco explorados como ferramentas preditivas em Paleontologia. Entretanto, considerando a natureza desafiadora e incerta da atividade de prospecção fóssil, modelos de paleodistribuição podem auxiliar na identificação de regiões com maiores chances de ocorrência da espécie ou grupo focal.

O nicho ecológico refere-se a um conjunto de condições e recursos disponíveis que permitem a sobrevivência e reprodução da espécie no ambiente e é formado por diversos aspectos ou condições de existência para as espécies no ambiente (*e.g.*, temperatura, solo, umidade, pH) e esses aspectos são classificados como diferentes tipos de nicho: nicho espacial que representa o espaço físico ocupado por um organismo; nicho trófico refere-se ao papel que o organismo desempenha na comunidade e nicho multidimensional que permite ao indivíduo sobreviver (Hutchinson, 1957; Odum, 2001; Soberon e Nakamura, 2009). Esse tipo de nicho,

multidimensional, é susceptível de medição, manipulação matemática e é subdividido em nicho fundamental referente a todas as condições e recursos disponíveis sem restrição, como por exemplo, restrição por competição e nicho realizado que é a faixa ambiental que a espécie realmente ocupa e recursos que utiliza sob restrições bióticas como predação, parasitismo, competição e disponibilidade de alimento (Hutchinson, 1957; Odum, 2001; Soberon e Nakamura, 2009).

A prática da Modelagem de Nicho Ecológico (ENMs - *Ecological Niche Models*) apresenta duas vertentes, de acordo com os aspectos ecológicos considerados: (i) nicho Grinnelliano definido por variáveis ambientais abióticas e condições ambientais em larga escala, como clima e geomorfologia; (ii) nicho Eltoniano realizado principalmente em escala local, é aplicado com interações bióticas e dinâmica recurso-consumidor (Soberón, 2007). No presente trabalho será adotado a ideia de nicho Grinnelliano, assim como na maioria dos trabalhos de paleodistribuição a partir da ENM, já que as interações bióticas e as relações entre recursos e consumidores ainda são esparsos e escassos para espécies extintas (porém ver Domingo *et al*., 2012; Pérez-Crespo *et al*., 2012; Bocherens, 2015; Dantas e Cozzuol, 2016; Bocherens *et al*., 2017; Dantas *et al*., 2017; Omena *et al*., 2020 para o recente avanço no entendimento da dinâmica recurso-consumidor).

Tradicionalmente, as pesquisas feitas com saídas de campo para prospecção fóssil, são realizadas em áreas onde já foram encontrados registros fósseis e identificadas a partir dos históricos dessas localidades. Outra alternativa são as buscas a partir das informações dos tipos e das idades das rochas expostas de certa região, que poderão ou não conter organismos fossilizados daquele período.

A combinação das projeções dos ENM's com algoritmos de priorização de áreas, tradicionalmente empregados em Biologia da Conservação para o ranqueamento ou priorização de áreas para criação de Unidades de Conservação (Moilanen, Leathwick e Elith, 2008), pode constituir um framework metodológico que permita otimizar os investimentos relacionados à prospecção fóssil.

Até a presente data, não foram encontrados na literatura trabalhos paleontológicos com o uso de metodologias de priorização de áreas para conservação ou combinando priorização de áreas e modelagem de distribuição, como uma ferramenta de determinação de áreas para prospecção de fósseis. Visto que uma das etapas da metodologia de priorização de áreas para conservação

baseia-se na distribuição das espécies, foi pensado no uso das modelagens de espécies extintas como uma potencial metodologia complementar para otimizar e auxiliar a busca por fósseis.

Diante disso, essa pesquisa tem como principal proposta uma nova abordagem que desenviesaria a tendência de retorno apenas à localidades já tidas como fossilíferas ampliando as possibilidades de áreas para prospecção, empregando a megafauna sul-americana como modelo de estudo. Assim, a relevância dessa pesquisa se dá por estudar uma nova forma de determinar regiões com grande potencial fossilífero, possibilitando a descoberta de novos sítios paleontológicos.

Esse trabalho está dividido em dois artigos apresentados nos capítulos 2 e 3, de maneira que o capítulo 2 (artigo 1) apresenta a modelagem de 14 espécies de animais da megafauna que viveram durante o Quaternário, com utilização de dados de registros de ocorrência dessas espécies para a América do Sul e camadas climáticas de mil em mil anos dentro de um intervalo temporal compreendido entre 23 mil anos até a idade mais recente que se tem registro datado dessas espécies. Já no capítulo 3 (artigo 2) apresenta o teste de uma metodologia para inferir possíveis áreas para prospecção fóssil. Foram utilizados os mapas das espécies gerados no artigo 1 com acréscimo de mapas de feições geológicas, geomorfológicas e sociais, para tentar prever as localidades potenciais para prospecção e comparar com as informações que já constam na literatura. O primeiro artigo será submetido à revista *Nature Communications* e o segundo artigo será submetido à revista *Quaternary Science Reviews*. As normas de submissão das revistas encontram-se nos anexos 1 e 2, respectivamente.

1.2 - Objetivos

Geral

Determinar regiões com potencial fossilífero, através do uso de dados de paleodistribuição das espécies e mapas físicos diversos da região de interesse, para indicar áreas prioritárias para busca de fósseis da megafauna.

Específicos

- Modelar nicho ecológico e gerar mapas de adequabilidade para espécies da megafauna quaternária na América do Sul, que serão tidos, grosso modo, como mapas de paleodistribuição das espécies.
- Elencar áreas prioritárias para prospecção de fósseis.

1.3 - Localização da área

Área de estudo

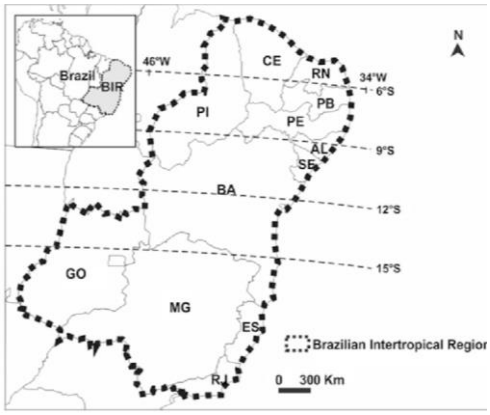
A América do Sul era composta por uma grande diversidade de espécies denominadas genericamente de megafauna quaternária, com ampla distribuição por boa parte do continente (Coltorti *et al.*, 2012; Ficcarelli *et al.*, 2003; França, 2014; Gallo *et al.*, 2013; González-Guarda *et al.*, 2017; Gutiérrez e Martínez, 2008; Varela *et al.*, 2018; Varela e Fariña, 2015). Grande parte da megafauna quaternária ocorreu na época Pleistoceno (2,58 – 0,011 Ma) e foi durante o Pleistoceno tardio que muitas espécies desse grupo se extinguiram no continente Sul Americano (Lima-Ribeiro e Diniz-Filho, 2013).

No Brasil, esse grupo esteve presente em todas as regiões do país, com destaque para a região Nordeste como uma região de maior concentração e diversidade. A Região Intertropical Brasileira (RIB) (FIGURA 1) é formada pelos estados do Nordeste (exceto Maranhão) juntamente com Goiás e os estados do Sudeste (exceto São Paulo). Cartelle (1999) definiu essa região como um domínio zoogeográfico com base na co-ocorrência de espécies de herbívoros e carnívoros nesta região. A maior parte dos registros fósseis nesses estados provêm de tanques naturais e cavernas (Dantas e Cozzuol, 2016).

Em Sergipe, um dos estados que fazem parte da RIB, há registros de ocorrências de diversos grupos paleontológicos de vertebrados da megafauna (Dantas, 2010; Dantas, 2012; Dantas *et al*., 2013; França *et al.*, 2011; França *et al*., 2013; França *et al.*, 2014; Dantas e Cozzuol, 2016; Dantas *et al.*,2017; Omena *et al*., 2020). Também nesse estado, tais registros são provenientes de municípios que apresentam feições geológicas naturais distintivas chamadas de tanques e também de cavernas (FIGURA 2). Os tanques naturais são recorrentes no Nordeste, se desenvolvem principalmente em rochas metamórficas tipo granitoides, em clima semiárido e são formados por meio de intemperismo físico-químico (Ximenes, 2009; Araújo-Júnior *et al.*, 2013; Araújo-Júnior, 2016).

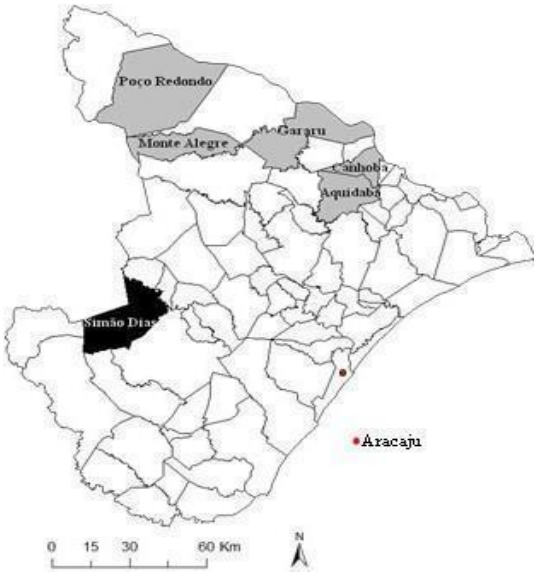
Neste trabalho a área de estudo pode ser dividida em duas porções. A primeira, em escala continental, onde serão modeladas as potenciais áreas de paleodistribuição da megafauna quaternária sul americana. A segunda, será delimitada em nível regional uma área dentro do estado de Sergipe, para um refinamento e definição das áreas prioritárias para prospecção.

FIGURA 1 – Localização da Região Intertropical Brasileira.



Fonte: Dantas e Cozzuol (2016) modificada de Cartelle (1999).

FIGURA 2 – Mapa de Sergipe com destaque para os municípios onde há registros de fósseis da megafauna. Em cinza os municípios com registros em tanques e em preto o município onde foram encontrados fósseis em caverna.



Fonte: Modificado de base cartográfica do IBGE.

1.4 - Métodos de trabalho

Mapas de adequabilidade:

Para modelagem de nicho e construção dos mapas de adequabilidade foram utilizados registros de ocorrências (coordenadas geográficas) de 14 espécies de herbívoros extintos da megafauna quaternária. Os dados de ocorrências utilizados para modelagem foram obtidos a partir da base de dados *The paleobiology database* (https://paleobiodb.org) e da literatura disponível. Além das informações sobre as espécies, foram utilizadas camadas climáticas a cada mil anos no intervalo de tempo de 23 mil anos até o recente (0 ka) e as informações sobre essas camadas foram obtidas no artigo de Carnaval *et al.* (2014).

As espécies consideradas para a modelagem foram: *Catonyx chiliensis* (=*Scelidodon chilensis*), *Catonyx cuvieri*, *Eremotherium laurillardi*, *Glossotherium robustum*, *Lestodon armatus*, *Megatherium americanum* e *Mylodon darwini* representativas de preguiças extintas; *Doedicurus clavicaudatus*, *Glyptodon clavipes*, *Holmesina occidentalis*, *Holmesina paulacoutoi*, *Neosclerocalyptus paskoensis* e *Pampatherium typus* entre os representantes de tatus e gliptodontes extintos; e *Notiomastodon platensis* representante de proboscídeo quaternário sulamericano extinto.

Os mapas de adequabilidade foram construídos com o *software Maxent* (versão 3.4.1) que se trata, basicamente, de um algoritmo de *Machine Learning*, capaz de relacionar dados de ocorrências das espécies com os conjuntos de variáveis climáticas para criar uma representação do nicho da(s) espécie(s) de interesse. Esse programa possui uma interface gráfica implementada em *JAVA* (Phillips, Anderson e Schapire, 2006) e, também, pode ser usado através de pacotes para o ambiente de programação *R* - por exemplo, *ENMeval* (Muscarella *et al.*, 2014) ou *biomod2* (Thuiller *et al.*, 2020). Os modelos gerados podem ser validados a partir de diferentes métricas de performance preditiva para modelos de *Machine Learning*, sendo que a mais usada é o AUC *(Area Under the* ROC *Curve*) (Jiménez-Valverde, 2012; Robin *et al*., 2011).

Para a avaliação dos modelos foi utilizado o método de Elith (2000), que considera os valores de AUCs maiores que 0,75 como potencialmente úteis para as análises ecológicas. Os modelos do *Maxent* foram gerados a partir da combinação de um conjunto de rotinas computacionais, implementadas com o auxílio de pacotes executados no ambiente de programação R (versão 3.4.4), com funções específicas para modelagem de dados geográficos, modelagem de distribuição das espécies, calibração, validação e análise de sensibilidade e incertezas dos modelos gerados.

Áreas prioritárias:

O *Zonation* (versão 4.0) — *software* que utilizamos para determinar as áreas prioritárias para prospecção — é um programa estatístico que analisa um conjunto de dados espaciais ou mapas digitais com informações associadas em cada pixel, produzindo uma classificação de prioridades regionais e descartando locais que levam à menor perda de diversidade, mantendo um grau de conectividade estrutural da área restante de acordo com as prioridades especificadas pelo pesquisador. Essa classificação das áreas é feita considerando a distribuição total e restante dos recursos utilizados nos dados de entrada para o programa e dos pesos dados a esses recursos

durante a etapa de configuração dos dados da análise (Di Minin, *et al.*, 2013; Moilanen *et al.*, 2005).

De acordo com Di Minin, *et al.*, 2014 são necessários três tipos de arquivos obrigatórios em todas as análises, que são: Arquivo de projeto (formato .bat); uma lista de recursos de biodiversidade e um arquivo de configurações de execução (formato .dat) que define os recursos analíticos que serão usados na classificação de prioridade. Com esse conjunto de arquivos para execução do *Zonation*, obtêm-se arquivos *outputs* com um mapa indicando melhores áreas para conservação das espécies estudadas (Kukkala e Moilanen, 2017; Lehtomäki e Moilanen, 2013; Tognelli *et al.*, 2011; Williams *et al.*, 2012), que são as denominadas "áreas quentes do mapa".

Neste estudo foram utilizados como arquivos de *input* para o programa, os mapas resultantes da modelagem de nicho de cada espécie, gerados com o *Maxent* que são apresentados em formato (TIFF), além de mapas geomorfológicos do Brasil com informações sobre desníveis, densidade rural e registros de cavernas no país.

Para definir quais áreas do mapa gerado seriam reconhecidas como prioritárias para prospecção, foi utilizada uma escala de cores que o próprio *Zonation* possui e gera para cada análise. Seguindo o padrão de cores "*Classic Zonation*" disponível nas configurações do programa, as áreas do mapa com as cores rosa, vermelho escuro e vermelho claro, dentro da área estudada, foram as regiões analisadas como sugestivas para prospecção e potencialmente fossilífera. Em seguida foi feito um recorte do mapa final na região do estado de Sergipe por ser uma área já conhecida com grande potencial fossilífero, para uma análise mais detalhada da região.

Por fim, as áreas indicadas como potencialmente fossilíferas foram sobrepostas a imagens de satélites a fim de se pontuar localidades com possíveis exposições rochosas para prospecção futura.

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CAPÍTULO 2 – “Mapping suitability patterns of the extinct Quaternary megafauna in South America: a new methodological approach”

Mapping suitability patterns of the extinct Quaternary megafauna in South America: a new methodological approach

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Abstract

Works on extinct species distribution modeling is largely based on the assumption that the values for environmental variables at fossil occurrence points can be computed from data layers for restricted geological periods. This work, through a methodological innovation, aims to build models with environmental information for the ages of the de facto fossils and, thus, to understand more continuously how the paleodistribution of 14 species of the South American megafauna varied, close to the time interval of its extinction. Distribution patterns were obtained for each of the fourteen analyzed species, with good predictive capacity for possible areas of suitability and with valid AUC results for the analyzes. With this new methodology we could simulate potential distribution patterns of extinct species near to their disappearance datum around the Pleistocene/Holocene boundary. A larger number of chronological data of other species could significantly increase the number of groups with potential to be analyzed.

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1 INTRODUCTION

The extinction events of the late Pleistocene diminished about 83% of the mammalian megafauna that lived in South America [1,2]. Therefore, South America is considered to have had the highest extinction index of these great animals. There is a great debate in relation to the extinction timing regarding this event, with some authors arguing that it occurred in specific regions and moments of the late Pleistocene [3], while others arguing that almost all as species simultaneously reduced on a continental scale [4].

The distribution of extinct species in specific time intervals is difficult to measure. The fossil records from collections, literature or databases show sparse and highly skewed occurrences in space and in time, since preservation depends on a combination of factors and specific environmental conditions conducive to preservation [5–8].

Distribution patterns can vary over time, expanding, retracting or moving according to the ecological characteristics of the species and environmental variations. One way to estimate the potential distribution of a species is to infer the geographic space that contains environmental conditions where it is known that the species occurred and that, therefore, are suitable for the establishment of its populations [9]. The mapping of these environmental conditions can be done through ecological niche modeling (ENM).

The research published so far, which worked with distribution modeling of extinct species (paleodistribution), focused on distributions in circumscribed periods such as Last Interglacial (130 - 115 ka) [10], Last Glacial Maximum (26,5 - 19 ka) [11] and Great Climate Holocene (8 - 5 ka) [12] or modeling only a few specific ages comprising one of these time intervals [13–18].

The present work, through a methodological innovation, aims to build data-driven models of extinct species considering estimates of the environmental variables for the ages actually registered for the fossil data and, thus, to understand in a more consistent way the dynamics of the paleodistribution of 14 species of the South American megafauna, close to the time interval of its extinction. We foresee a possibility where there is no relationship between

climatic variations and the absence of dated fossil records for each species (e.g., modeled paleodistribution of a species at a time whose fossil record indicates that it would be extinct). Another possibility will be considered when the paleodistribution - therefore, also the climatic variations - is in line with the physical records, geographically and temporally. Within this possibility, we predict two situations: a first in which each species will have an independent biogeographic behavior (e.g., regional species specific extinctions); and a second, when, at a given time, there is a sudden change in the paleodistribution of most of the species considered (e.g., extinction on a larger scale).

2 MATERIAL AND METHODS

2.1 Data collection

Fossil occurrence records from the entire South American continent, regarding 14 species of herbivores were used (Table 1). The occurrence records used herein were taken from the literature (see Supplementary Table 1 in Supplementary Table 1). In addition to these records, paleoclimatic simulations were also used dating every 1 ka, in a time interval between 23 ka until the age at which there is the most recent dated record assumed for each species (Table 1 and see Supplementary Table 2). The paleoclimatic layers were obtained from [19].

Table 1: **List of studied species, assumed time interval of existence and modeled interval that comprises the period of the modeled average map for each species.**

Species	Time interval (ka)	Modeled interval (ka)
Catonyx chilensis (=*Scelidodon chilensis*)	44 to 8	23 to 8
Catonyx cuvieri	42 to 11	23 to 11
Doedicurus clavicaudatus	30 to 6	23 to 6
Eremotherium laurillardi	48 to 8	23 to 8
Glossotherium robustum	42 to 11	23 to 11
Glyptodon clavipes	58 to 10	23 to 10
Holmesina occidentalis	41 to 13	23 to 13
Holmesina paulacoutoi	52 to 11	23 to 11
Lestodon armatus	120 to 10	23 to 10
Megatherium americanum	58 to 6	23 to 6
Mylodon darwini	80 to 13	23 to 13

Neosclerocalyptus paskoensis	58 to 8	23 to 8
Notiomastodon platensis	530 to 6	23 to 6
Pampatherium typum	58 to 6	23 to 6

Taxonomically, the studied species are mammalians comprised in three orders: Pilosa represented by the sloths *Catonyx cuvieri*, *Catonyx chilensis*, *Eremotherium laurillardi*, *Glossotherium robustum*, *Lestodon armatus, Megatheirum americanum* and *Mylodon Darwini*; Cingulata represented by armadillos and glyptodonts *Doedicurus clavicaudatus*, *Glyptodon clavipes*, *Holmesina occidentalis, Holmesina paulacoutoi*, *Neosclerocalyptus paskoensis* and *Pampatherium typus;* and Proboscidea represented by a single taxon, *Notiomastodon platensis*.

2.2 Suitability maps

Maxent was used for niche modeling. This software implements a machine learning algorithm derived from maximum entropy theory[20]. To implement models with Maxent, we rely on R language, through the packages ENMeval [21]. While using Maxent, it is possible to implement data-driven models from partial data (i.e., presence data only), by replacing true absence data with uniformly distributed background points [22]. This software is used for both modeling extant species [23,24] and through combining fossil and extant species records The latter is the most commonly used methodology when it involves fossil groups [25–28] together with environmental information, since studies integrating only fossil information with ENMs are still scarce (but see [29–31]).

Many authors have published work over the past decade using niche modeling to investigate the distribution of species [9,16,32]. Among the models used for niche modeling, such as General Linear Model (GLM), Random Forest and Maxent, the latter presented the best performance [33–36], justifying the use of this software, at present work. Thus, in this work Maxent (version 3.4.1) was used, combining species occurrence data and layers of climatic variables in order to obtain suitability models for the focal species. The entire modeling process was conduced with *biomod2* package in the R programming environment (version 3.4.4).

The generated models were validated using the analysis of the Area Under the ROC Curve, or AUC. The ROC curve is obtained from the sensitivity and specificity values computed for a sequence of decision thresholds. Values of AUC = 1 indicate perfect predictive performance, while AUC = 0.5 indicates that the model has a predictive performance no higher than a purely random classifier [2]. Values of AUC > 0.75 are potentially useful for ecological analyzes [37].

By using the obtained models, maps were produced for each species, using information from the climatic layers for South America. The Maxent software built minimum, average and maximum maps, so that the present work considered the average maps, as representative of areas of potential distribution of each of the analyzed species.

In order to avoid the exclusion of occurrence data whose ages were undetermined, instances were created with a set of hypothetical ages, sampled within the range of possible ages for the species (column "Time interval", in Table 1). For example, a record of the occurrence of *Eremotherium laurillardi* in a given location that has absolute dating is directly used in the model, whereas for another record of *E. laurillardi*, for which there is no known absolute age, a number instances were generated, each of which had an age inferred drawn within the plausible range known for the species (ie, between 48 and 8 thousand years, for *E. laurillardi*). For these records, hypothetical ages were assumed, comprising the time interval of existence reported in the literature for each species (Table 1). For each record with an unknown age, a set of instances was generated, each of which results in its own projection model. Subsequently, each point is analyzed in relation to the degree of uncertainty that its drawn age generates for the projection model. That is, some occurrences, even assuming ages as diverse as 8 thousand or 23 thousand years, do not generate major changes in the projected model. Points of this type were maintained, assuming that, regardless of what age they are, little variation brings to the final model. The number of instances (number of ages drawn, for

occurrences with unknown ages) was statistically defined so that it was 50% greater than the total number of occurrence points of each species.

The uncertainty of each instance was calculated based on a partial correlation between predictive performance metrics (here, AUC and TSS) and the age range drawn for a specific point. After eliminating the instances whose drawn ages generated a lot of uncertainty in their projections, it was then possible to create the suitability maps projected for the ages of interest from the average of the projection maps of all maintained instances. For example, to create a suitability map with a projection of interest in 12 thousand years, for *E. laurillardi*, projections for that age are generated with each of the instances that passed the uncertainty test, say 70 instances. In the present work, the average of these 70 individual projections generated was assumed as the final suitability map projected for 12 thousand years.

This procedure was done for all ages of interest to be projected (column "Modeled interval", in Table 1). Thus, a fossil record with no absolute age assigned was simulated as being able to present any of the ages within the range of occurrence listed in Table 1, as long as it did not generate too much noise in the modeling. Such a procedure generates greater robustness to the results for allowing the consideration of a greater number of occurrences, without at the same time bringing great uncertainties to the projections.

Individual maps for each millennium were projected within each range of existence close to the extinction of each species (Table 1). In addition, an average map for each species was also generated from these individual maps using the mean function of the raster package in software R (version 3.4.4). These average maps were assumed to represent the average potential area for the probable distribution of each species along each modeled interval.

3 RESULTS AND DISCUSSION

The performance of the models, estimated using the AUC values, was high for all species. All projections showed AUC with values above 0.75 (see supplementary Table 3), which can be considered as ecologically informative [37]. Figure 1 shows the average maps (see table 1 to

check the period of the average map) resulting for each species. The areas that have a green color pattern are the areas where the species would find better climatic conditions to exist. It can be seen that among the 14 herbivore species studied, 10 showed a trend towards more suitable areas similar to each other, with an adequacy pattern restricted mainly to the southern part of the continent.

When analyzing the maps separately, according to the mammalian orders, it was possible to observe that of the seven species of the order Pilosa, four of them (ie, *G. robustum* (Fig. 1f), *L. armatus* (Fig. 1i), *M. americanum* (Fig. 1j) and *M. darwini* (Fig. 1k)) showed similar areas of suitability in the southernmost portion of the continent.This pattern of distribution coincides with studies of occurrences of these species and available in the literature [17,38–41]. The other three species of Pilosa showed a different distribution pattern (C. chilensis (Fig. 1a), C. cuvieri (Fig. 1b), E. laurillardi (Fig. 1d)). It is worth highlighting the pattern presented for *C. cuvieri*, which was broader in practically the entire continent except the Northern region of Brazil (Fig. 1b), corroborating the pattern found by [42]. *Catonyx chilensis* showed a more restricted distribution pattern and predominantly in Chile and Peru (Fig. 1a) and according to [43] and [44] there are also records of occurrences of this species in Argentina and in Bolivia.

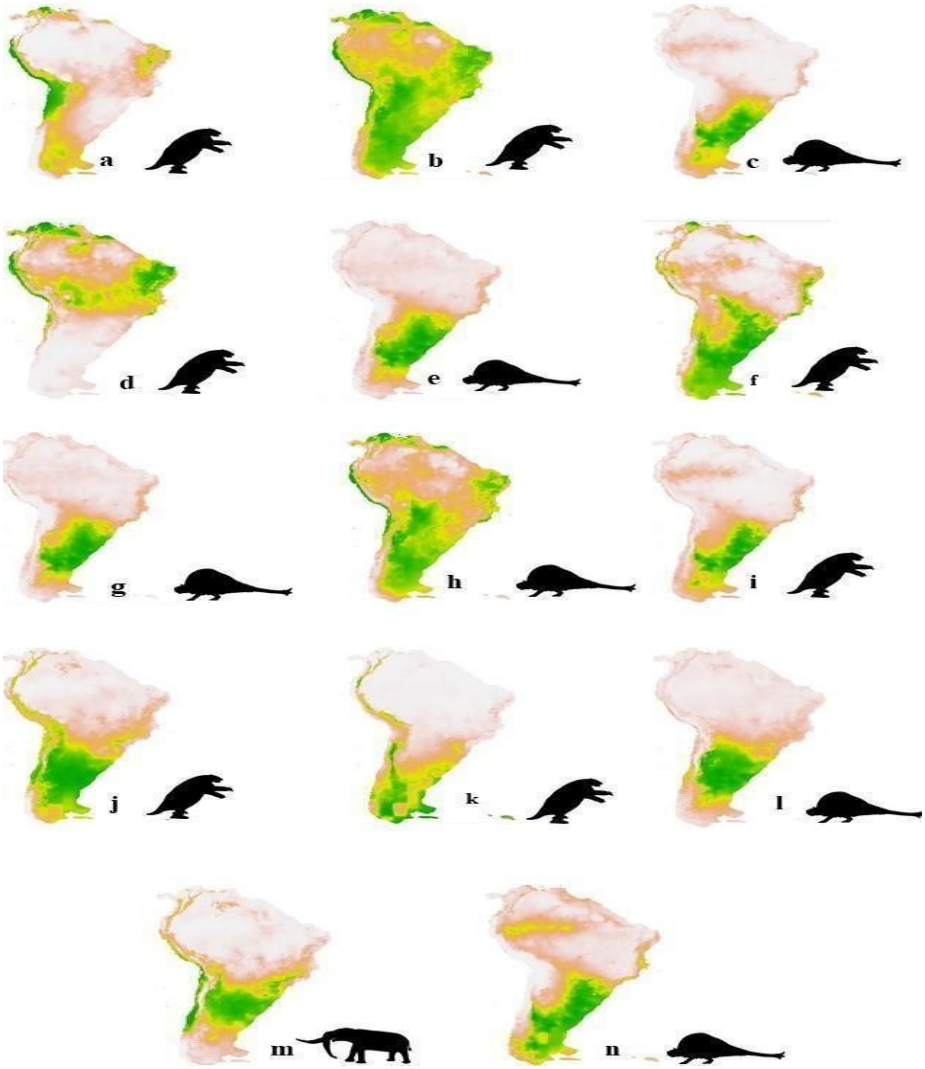

Figure 1 Average maps and suitability areas modeled for megafauna herbivores. Green regions represent the most suitable areas for the species. a- *Catonyx chiliensis*; b- *Catonyx cuvieri*; c- *Doedicurus clavicaudatus*; d- *Eremotherium laurillardi*; e- *Glyptodon clavipes*; f- *Glossotherium robustum*; g- *Holmesina occidentalis*; h- *Holmesina paulacoutoi*; i- *Lestodon armatus*; j- *Megatherium americanum*; k- *Mylodon darwini*; l- *Neosclerocalyptus paskoensis*; m- *Notiomastodon platensis*; n- *Pampatherium typus*.

For the Cingulata order in which six species were studied, almost all showed the same pattern of distribution prevalent in the south of the continent (Fig. 1c, 1e, 1g, 1h, 1l, 1n), but according to [45,40,46–48] these species also occur in other countries such as Brazil, Peru and Venezuela. The only Cingulata species that had a wider distribution was *H. paulacoutoi*, which besides being present in the southern part of the continent, also had a good distribution in the Northeast of Brazil and in the Andes region (Fig. 1h). This pattern is compatible with the data published by [39,47–49]. Interpreting the maps generated in the present work, all species

of the order Cingulata could co-occur in the South portion of South America if considering only climatic suitability.

Notiomastodon plantensis, representative of the order proboscidea, presented an average map of the suitability areas that showed that this species found better conditions for survival in the southernmost region of Brazil, northern Argentina, in addition to the countries of Uruguay and Chile (Fig.1m). This result differs from the geographic distribution found for this species in the literature. In studies that studied the distribution of this species, as well as other representatives of that order, *N. plantensis* is widely distributed across the continent, with occurrences in all South American countries [50–52]. However, it is worth noting that some records are referred to *N. platensis* even without presenting the diagnostic characteristics for the species, simply because it is the only species described for the genus (see discussion in [53]). One possibility we have raised is that more than one species of proboscid, in addition to *Notiomastodon platensis* and *Cuvieronius hyodon*, may have existed on the South American continent at the end of the Quaternary.

Catonyx cuvieri was the species that resulted in the largest area of suitability across the continent, indicating that it would possibly be the species that would best adapt in almost all regions of South America (Fig. 1b), this result corroborates the description of occurrences cited by [42]. The species *Lestodon armatus*, on the other hand, showed a more restricted suitability than the other species and predominantly in the southern portion of Brazil, in Uruguay and in part of Argentina (Fig. 1i), a result also found in the survey of occurrences made by [17].

The orders Pilosa and Cingulata are part of the superorder Xenarthra, which represents a group of placental mammals. The species *Doedicurus clavicaudatus*, *Megatherium americanum* and *Pampatherium typus*, may present fossil records dated as recent as 6 thousand years ago and observing the individual suitability maps of these species for this age,

it was observed that they may have coexisted in the moments close to their extinction, in the southern region of the continent, mainly in Uruguay, Argentina and the southern region of Brazil (Fig.2). [18] made a "unitemporal" analysis (where all occurrences of a certain fossil species are grouped at a single age, to obtain the values for the climatic variables of the modeling) and obtained similar results when modeling the niche of *D. clavicaudatus, M. americanum* and *P. typus* with data for the Holocene Optimal Climate (HCO) (compare Fig. 2 with Figs 1 and 2 from [18]).

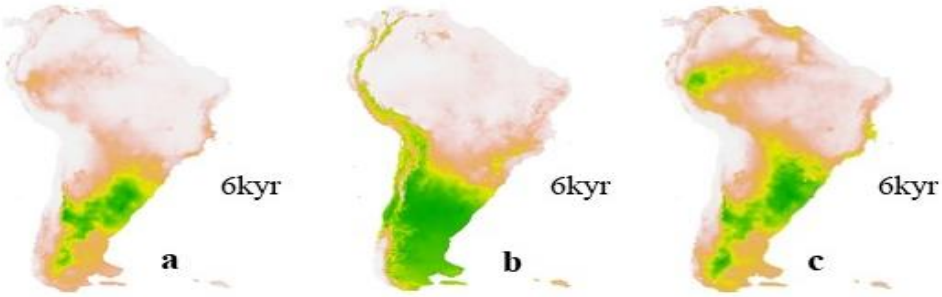

Figure 2 Individual maps of the species with the most recent record dated 6 thousand years ago. The darker-colored regions of the maps represent the most suitable areas for the species. a- *Doedicurus clavicaudatus*, b- *Megatherium americanum*, c- *Pampatherium typus*.

During the Pleistocene, the South American continent could be divided into four main vegetation patterns: Open savanna; mosaic of open forests and savannas; pasture/steppe; cold desert/steppe (see [54]). According to the species suitability standards, it is noted that they did not show a good adaptation in large areas where the vegetation pattern was that of open Savanna. These results agrees with the considerations of [55]. Observing a more detailed vegetation pattern during the Last Glacial Maximum (25,000-15,000 BP), as presented in [56], we observed that the species studied here did not find suitable climatic conditions in tropical forest, tropical pasture and savanna.

Several authors point to the drastic climatic changes that occurred during the late Pleistocene and beginning of the Holocene, which caused changes in vegetation, as one of the ecological causes of the extinction of these mega herbivores that inhabited South America [55] and [57]). Such extinction would have continued changes in vegetation, due to the absence of these large

dispersers, also affecting the physical and trophic structure of the ecosystem, species composition, biogeochemistry and even climate [58–60]. The species in Figure 3 were chosen after observing, within the taxonomic order to which they belong, which obtained the greatest reduction in area in the last three thousand years of records. Our data (Fig. 2, Fig. 3 and see Supplementary Date 1) do not show drastic reductions in the areas of suitability of the species analyzed here, in their last thousands of years of existence. Although the reduction of these areas is evident in some of the cases (Fig. 3), areas suitable for the existence of these species always remained available.

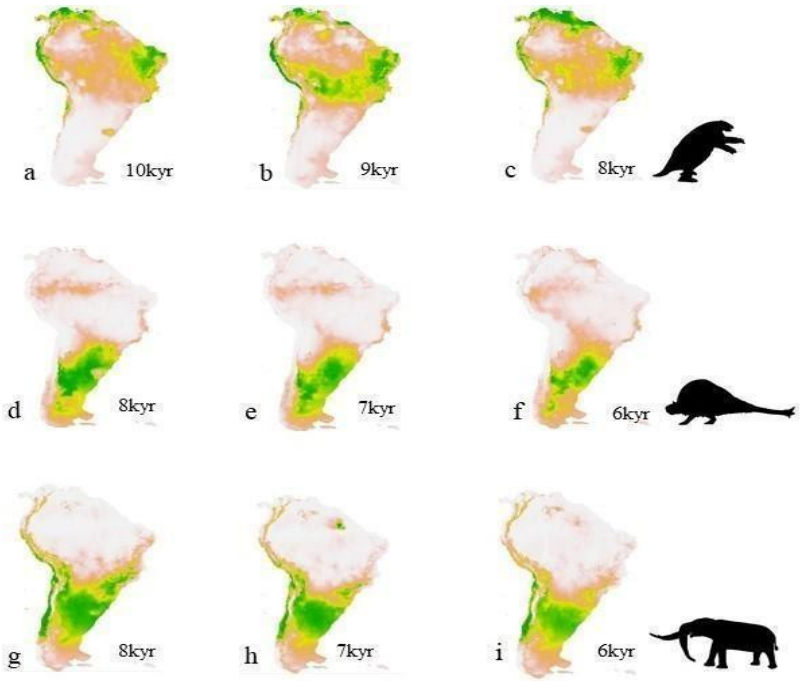

Figure 4 Modeled maps for the last three thousand years of registration. a, b, c - *Eremotherium laurillardi*; d, e, f - *Doedicurus clavicaudatus*; g, h, i - *Notiomastodon platensis*.

In the maps of *E. laurillardi* in Fig 3, we can see that there was a reduction in the area that corresponds to the Central-Westregion of Brazil, but an expansion in the northernmost area of the continent (Fig. 3c). For *D. clavicaudatus*, regions with enlarged areas were not observed, only a reduction in the area to the south of Argentina (Fig. 3f). *N. platensis*, as well as the species of the order Cingulata, did not present new areas of suitability and it is possible to

observe a small reduction mainly in the South of Brazil (Fig. 3i). The species that showed the most significant reduction was *E. laurillardi*, but as there was an increase in area, we cannot consider that they were very drastic changes so that it could influence the extinction of this species, as well as none of the other species studied.

Thus, our results do not suggest that climate change was the only agent responsible for the extinction of the South American megafauna, at the end of the Pleistocene beginning of the Holocene.

4 CONCLUSIONS

In this article, the megafauna group studied showed similar distribution patterns between species, with good predictive capacity for possible areas of suitability. In view of the results obtained, we can consider this methodology as valid, since the resulting patterns of suitability corroborate with the vegetation preferences of these species during the Pleistocene and with the areas of occurrence records available in the literature.

It is noteworthy that of the 14 species studied, *Notiomastodon platensis* was the one that showed the most significant divergent results in relation to what is found in the literature. Considering that some records are attributed to this species just because it is the only one of its kind described for the continent, it is important to consider a more in-depth analysis of these records in order to compare them with the diagnostic characteristics of this species. From this new analysis, it will be possible to confirm whether they are correctly attributed to *Notiomastodon platensis* or if they are records of another species of proboscid.

According to the predictions that we hypothesized initially, we conclude that the first situation, where each species would present an independent biogeographic behavior, has materialized. Observing the average maps (Fig.1) with the exception of *Catonyx chilensis* and *Eremotherium laurillardi*, the species showed a common pattern in the southern portion of the continent, but each species presented distinct areas restricted only to the south of the continent

or larger distributed by other regions. Analyzing the individual maps every thousand years resulting from each species, no drastic changes were observed in the areas of suitability, exept for only small reductions in these areas, in some cases. The species *Catonyx chiliensis*, *Eremotherium laurillardi*, *Megatherium americanum* and *Notiomastodon platensis*, showed changes in the suitable areas over the years that could indicate the extinction of these species in a certain region, but remained present in other regions. The species *Pampatherium typus* initially presented the southern region of the continent as more suitable and over the years other areas have emerged, such as in Peru and part of the Amazon region.

In the second predicted hypothesis, where a specific temporal moment of sudden changes in the paleodistribution of most of the considered species could occur, it did not sustain. Analyzing the species maps in the common range of 23 ka to 13 ka, in which there are records of occurrences for all species, there was no age with sudden reductions in the areas of species suitability, but we highlight the age of 13 ka where nine of the 14 species showed a reduction in some area.

All species still showed areas of suitability in the last thousand modeled years where there were records in the literature of the analyzed taxon fossils. Since the maps were modeled every thousand years and no abrupt changes were evident, we cannot consider that climatic changes and consequent changes in vegetation were the main factors responsible for the extinction of these species.

Finally, we see a potential for expanding the data to include records of more extinct species, such as carnivores, or small sized mammals, such as rodents, or even other taxonomic groups, such as crocodiles and other reptiles, as more of these occurrences become available. A larger number of chronological data could also significantly increase the resolution of the results and the number of groups with the potential to be analyzed as it was done in this work.

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Author's contributions:

W.S.A, A.L, P.A.M and A.A.E designed the study, executed the project and prepared the manuscript; M.A.D.T contributed with surveys of occurrence records, construction of species maps and critically reviewed the manuscript; P.A.M contributed to the treatment of the modeled maps and critically reviewed the manuscript.

Competing interest

The authors declare no competing interests.

ANEXOS DO ARTIGO 1

Supplementary Table 1-Occurrence records used in the work

Species	Longitude	Latitude	Cal. Mean	SD	Reference
Catonyx chilensis	-81,262443	-4,581216			Varela et al. 2017
Catonyx chilensis	-74,210395	-13,161481			Varela et al. 2017
Catonyx chilensis	-75,376111	-12,2475			Varela et al. 2017
Catonyx chilensis	-64,736275	-21,5368			Varela et al. 2017
Catonyx chilensis	-79,334585	-7,46378	16000		Varela et al. 2017
Catonyx chilensis	-69,700594	-34,157275			Varela et al. 2017
Catonyx chilensis	-79,543971	-7,322969			Varela et al. 2017
Catonyx cuvieri	-53,332206	-33,5699			Varela et al. 2017
Catonyx cuvieri	-55,659444	-34,270278			Varela et al. 2017
Catonyx cuvieri	-57,880651	-34,419852			Varela et al. 2017
Catonyx cuvieri	-41	-3,1			Varela et al. 2017
Catonyx cuvieri	-48,735652	-24,541596			Varela et al. 2017
Catonyx cuvieri	-42,607157	-8,91949	12850		Varela et al. 2017
Catonyx cuvieri	-40,860518	-10,160643	22000		Varela et al. 2017
Catonyx cuvieri	-44,113041	-19,514262			Varela et al. 2017
Doedicurus clavicaudatus	-61,541667	-39,003611			Varela et al. 2017
Doedicurus clavicaudatus	-56,0425	-34,6175	30000		Varela et al. 2017
Doedicurus clavicaudatus	-59,109167	-38,211389	15500	5500	Varela et al. 2017
Doedicurus clavicaudatus	-60,2574651	-36,88978	15500	5500	Varela et al. 2017
Doedicurus clavicaudatus	-58,718611	-35,7225	15500	5500	Varela et al. 2017
Doedicurus clavicaudatus	-61,683333	-38,566667			Varela et al. 2017
Doedicurus clavicaudatus	-60,076389	-37,134444			Varela et al. 2017
Doedicurus clavicaudatus	-59,115556	-38,196667	13000	500	Varela et al. 2017
Doedicurus clavicaudatus	-53,332206	-33,5699			Varela et al. 2017
Doedicurus clavicaudatus	-64,295311	-36,622303			Varela et al. 2017
Doedicurus clavicaudatus	-60,630833	-33,008611			Varela et al. 2017
Doedicurus clavicaudatus	-56,306325	-34,706741	17620		Varela et al. 2017
Doedicurus clavicaudatus	-58,763056	-35,742222	12860		Varela et al. 2017
Eremotherium laurillardi	-65,325278	-10,050278			Varela et al. 2017

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Eremotherium laurillardi	-79,543971	-7,322969		Varela et al. 2017
Eremotherium laurillardi	-41,144136	-10,8273		Varela et al. 2017
Eremotherium laurillardi	-81,133333	-4,65	13900	Varela et al. 2017
Eremotherium laurillardi	-40,766408	-10,973121		Varela et al. 2017
Eremotherium laurillardi	-43,887567	-19,645389		Varela et al. 2017
Eremotherium laurillardi	-73,38	-0,6		Varela et al. 2017
Eremotherium laurillardi	-72,32	-10,15		Varela et al. 2017
Eremotherium laurillardi	-68,55	-8,05		Varela et al. 2017
Eremotherium laurillardi	-57	-15,33		Varela et al. 2017
Eremotherium laurillardi	-37,73	-5,62		Varela et al. 2017
Eremotherium laurillardi	-49	-24,63		Varela et al. 2017
Eremotherium laurillardi	-42,5	-8,5		Varela et al. 2017
Eremotherium laurillardi	-56	-3,3	11340	Varela et al. 2017
Eremotherium laurillardi	-70	9,62	10710	Varela et al. 2017
Eremotherium laurillardi	-80,8	-2,2	8680	Varela et al. 2017
Eremotherium laurillardi	-40,55	-11,18	15000	Varela et al. 2017
Eremotherium laurillardi	-48,594876	-24584		Varela et al. 2017
Eremotherium laurillardi	-36,449181	-6,225088	18000	Varela et al. 2017
Eremotherium laurillardi	-41	-3,1	26000	Varela et al. 2017
Eremotherium laurillardi	-39,209423	-10,752495	18000	Varela et al. 2017
Eremotherium laurillardi	-53,332206	-33,5699		Varela et al. 2017
Eremotherium laurillardi	-42,607157	-8,91949	10000	Varela et al. 2017
Eremotherium laurillardi	-80,883333	-2,216667	23560	Varela et al. 2017
Eremotherium laurillardi	-40,799672	-10,928398	16100	Auler et al. 2006
Eremotherium laurillardi	-48,71666667	-4,583333333	15130	Hube et al. 2013
Eremotherium laurillardi	-56,01388889	-4,250472222	135175	Rossetti et al. 2004
Eremotherium laurillardi	-36,57547222	-6,178638889	27190	Dantas et al. 2013
Eremotherium laurillardi	-37,68427778	-9,782861111	18715	Dantas et al. 2013
Eremotherium laurillardi	-37,75361111	-9,926944444	128775	França et al. 2014
Eremotherium laurillardi	-37,75361111	-9,926944444	12892	França et al. 2014
Eremotherium laurillardi	-37,75361111	-9,926944444	111585	França et al. 2014
Eremotherium laurillardi	-37,75361111	-9,926944444	11163	França et al. 2014

Continuação...

Eremotherium laurillardi	-37,75361111	-9,926944444	13436		França et al. 2014
Eremotherium laurillardi	-80,88333333	-2,216666667	23560		Lindsey e Lopez 2005
Eremotherium laurillardi	-97,67083333	-18,19555556	27610		Vallverdú et al. 2017
Eremotherium laurillardi	-37,75361111	-9,926944444	12652		Dantas et al. 2014
Eremotherium laurillardi	-37,75361111	-9,926944444	12535		Dantas et al. 2017
Eremotherium laurillardi	-35,92064167	-5,951066667	11565		Dantas et al. 2017
Eremotherium laurillardi	-37,92583333	-10,01083333	13373		Dantas et al. 2017
Eremotherium laurillardi	-80,691533	8,398195	44840		Pearson 2005
Eremotherium laurillardi	-80,695076	7,979778	47040		Pearson 2005
Eremotherium laurillardi	-80,695076	7,979778	21490		Pearson 2005
Glossotherium robustum	-58,488132	-37,152623			Varela et al. 2017
Glossotherium robustum	-56,0425	-34,6175	30000		Varela et al. 2017
Glossotherium robustum	-60,511054	-33,155731	12000		Varela et al. 2017
Glossotherium robustum	-60,322945	-36,888807			Varela et al. 2017
Glossotherium robustum	-56,449766	-30,383379			Varela et al. 2017
Glossotherium robustum	-53,332206	-33,5699			Varela et al. 2017
Glossotherium robustum	-81,262443	-4,581216	14000	400	Varela et al. 2017
Glossotherium robustum	-58,780764	-38,161487	11000		Varela et al. 2017
Glossotherium robustum	-61,683333	-38,566667			Varela et al. 2017
Glossotherium robustum	-58,718611	-35,7225			Varela et al. 2017
Glossotherium robustum	-69,54464	11,482199	15300	1000	Varela et al. 2017
Glossotherium robustum	-59,109167	-38,211389			Varela et al. 2017
Glossotherium robustum	-56,45	-30,433333			Varela et al. 2017
Glossotherium robustum	-77,951785	0,71473			Varela et al. 2017
Glossotherium robustum	-56,866444	-29,672381			Varela et al. 2017
Glossotherium robustum	-56,545969	-15,332175			Varela et al. 2017
Glossotherium robustum	-69,522202	11,499191			Varela et al. 2017
Glossotherium robustum	-64,736275	-21,5368			Varela et al. 2017
Glossotherium robustum	-56,866799	-29,671958			Varela et al. 2017
Glyptodon clavipes	-56,866444	-29,672381	14925		Varela et al. 2017
Glyptodon clavipes	-68,585194	10,858417			Varela et al. 2017
Glyptodon clavipes	-58,67058	-26,623531	58000		Varela et al. 2017

Continuação...

Glyptodon clavipes	-67,863801	-33,417861			Varela et al. 2017
Glyptodon clavipes	-61,541667	-39,003611			Varela et al. 2017
Glyptodon clavipes	-61,683333	-38,566667			Varela et al. 2017
Glyptodon clavipes	-58,233333	-38,433333			Varela et al. 2017
Glyptodon clavipes	-35,726389	-35,504167			Varela et al. 2017
Glyptodon clavipes	-58,718611	-35,7225			Varela et al. 2017
Glyptodon clavipes	-56,0425	-34,6175	30000		Varela et al. 2017
Glyptodon clavipes	-56,45	-30,433333			Varela et al. 2017
Glyptodon clavipes	-59,109167	-38,211389			Varela et al. 2017
Glyptodon clavipes	-57	-31,25			Varela et al. 2017
Glyptodon clavipes	-48,735652	-24,541596			Varela et al. 2017
Glyptodon clavipes	-42,607157	-8,91949			Varela et al. 2017
Glyptodon clavipes	-53,332206	-33,5699			Varela et al. 2017
Glyptodon clavipes	-60,2574651	-36,88978			Varela et al. 2017
Glyptodon clavipes	-62,424203	-62,096147			Varela et al. 2017
Glyptodon clavipes	-60,076389	-37,134444			Varela et al. 2017
Glyptodon clavipes	-57,966667	-29,666667	14850	50	Varela et al. 2017
Glyptodon clavipes	-56,866799	-29,671958			Varela et al. 2017
Glyptodon clavipes	-64,295311	-36,622303			Varela et al. 2017
Glyptodon clavipes	-56,306325	-34,706741	17620		Varela et al. 2017
Holmesina occidentalis	-80,883333	-2,216667	23560		Varela et al. 2017
Holmesina occidentalis	-81,262443	-4,581216	13500	500	Varela et al. 2017
Holmesina occidentalis	-68,585194	10,858417			Varela et al. 2017
Holmesina occidentalis	-80,923298	-2,225713			Varela et al. 2017
Holmesina occidentalis	-79,334585	-7,46378	16000		Varela et al. 2017
Holmesina paulacoutoi	-40,766408	-10,973121	15000		Varela et al. 2017
Holmesina paulacoutoi	-53,332206	-33,5699			Varela et al. 2017
Holmesina paulacoutoi	-40,924582	-8,482249	14900	3600	Varela et al. 2017
Holmesina paulacoutoi	-56,866799	-29,671958	13750	2750	Varela et al. 2017
Holmesina paulacoutoi	-64,362522	-27,650939	19900		Varela et al. 2017
Lestodon armatus	-56,0425	-34,6175	30000		Varela et al. 2017
Lestodon armatus	-60,2574651	-36,88978			Varela et al. 2017

Continuação...

Lestodon armatus	-53,332206	-33,5699		Varela et al. 2017
Lestodon armatus	-58,718611	-35,7225		Varela et al. 2017
Lestodon armatus	-59,109167	-38,211389		Varela et al. 2017
Lestodon armatus	-56,45	-30,433333		Varela et al. 2017
Lestodon armatus	-64,736275	-21,5368		Varela et al. 2017
Lestodon armatus	-56,267171	-34,752766	17500	Varela et al. 2017
Lestodon armatus	-57,880651	-34,419852	12000	Varela et al. 2017
Lestodon armatus	-60,737062	-38,323129		Varela et al. 2017
Lestodon armatus	-48,735652	-24,541596		Varela et al. 2017
Megatherium americanum	-58,67058	-26,623531	58000	Varela et al. 2017
Megatherium americanum	-76,376876	-12,20643		Varela et al. 2017
Megatherium americanum	-81,262443	-4,581216		Varela et al. 2017
Megatherium americanum	-74,210395	-13,161481		Varela et al. 2017
Megatherium americanum	-73,542903	-13,298548		Varela et al. 2017
Megatherium americanum	-64,736275	-21,5368		Varela et al. 2017
Megatherium americanum	-68,366667	-34,75		Varela et al. 2017
Megatherium americanum	-56,866799	-29,671958		Varela et al. 2017
Megatherium americanum	-60,384722	-37,01		Varela et al. 2017
Megatherium americanum	-60,511054	-33,1557312		Varela et al. 2017
Megatherium americanum	-60,076389	-37,134444	7000	Varela et al. 2017
Megatherium americanum	-59,18215	-38,184848		Varela et al. 2017
Megatherium americanum	-69,59621	-35,468105		Varela et al. 2017
Megatherium americanum	-64,295311	-36,622303		Varela et al. 2017
Megatherium americanum	-68,366667	-34,75		Varela et al. 2017
Megatherium americanum	-66,083333	-33,133333		Varela et al. 2017
Megatherium americanum	-59,109167	-38,211389		Varela et al. 2017
Megatherium americanum	-58,718611	-35,7225		Varela et al. 2017
Megatherium americanum	-60,2574651	-36,88978		Varela et al. 2017
Megatherium americanum	-58,233333	-38,433333		Varela et al. 2017
Megatherium americanum	-61,683333	-38,566667		Varela et al. 2017
Megatherium americanum	-57,193115	-30,171903		Varela et al. 2017
Mylodon darwini	-56,0425	-34,6175	30000	Varela et al. 2017

Continuação...

Mylodon darwini	-53,332206	-33,5699				Varela et al. 2017
Mylodon darwini	73,7052	-38,211389				Varela et al. 2017
Mylodon darwini	-32,604285	-57,657868	12000			Varela et al. 2017
Mylodon darwini	-70,168513	-52,763549				Varela et al. 2017
Mylodon darwini	-70,004567	-51,992948	28600			Varela et al. 2017
Mylodon darwini	-72,613229	-51,572655				Varela et al. 2017
Mylodon darwini	-69,744594	-52,089039	13200		200	Varela et al. 2017
Mylodon darwini	-72,564673	-51,531204	13400			Varela et al. 2017
Mylodon darwini	-72,6	-51,566667	13000			Varela et al. 2017
Mylodon darwini	-70,049944	-52,033053	12500			Varela et al. 2017
Mylodon darwini	-72,604743	-53,5696	13500			Varela et al. 2017
Mylodon darwini	-72,619212	-51,564256	12600			Varela et al. 2017
Mylodon darwini	-71,490266	-31,92763	13500			Varela et al. 2017
Mylodon darwini	-58,033333	-31,416667				Varela et al. 2017
Mylodon darwini	-68,366667	-34,75				Varela et al. 2017
Mylodon darwini	-70,174444	-51,747778				Varela et al. 2017
Mylodon darwini	-69,737952	-52,11423	8600			Varela et al. 2017
Mylodon darwini	-67,867778	-47895	13000			Varela et al. 2017
Mylodon darwini	-64,495816	-31,714782	26000			Varela et al. 2017
Neosclerocalyptus paskoensis	-59,112488	-34,568241				Varela et al. 2017
Neosclerocalyptus paskoensis	-62,75	-37,183333				Varela et al. 2017
Neosclerocalyptus paskoensis	-59,651445	-33,672877				Varela et al. 2017
Neosclerocalyptus paskoensis	-58,233333	-38,433333				Varela et al. 2017
Neosclerocalyptus paskoensis	-34,563281	NA				Varela et al. 2017
Neosclerocalyptus paskoensis	-65,276241	-26,11122				Varela et al. 2017
Neosclerocalyptus paskoensis	-62,424203	-62,096147				Varela et al. 2017
Neosclerocalyptus paskoensis	-63,050977	-31,417879				Varela et al. 2017
Neosclerocalyptus paskoensis	-60,7	-32,7				Varela et al. 2017
Neosclerocalyptus paskoensis	-65,257774	-26,733045				Varela et al. 2017
Neosclerocalyptus paskoensis	-65,205692	-26,831053				Varela et al. 2017
Neosclerocalyptus paskoensis	-58,67058	-26,623531	58000	#VALOR!		Varela et al. 2017
Neosclerocalyptus paskoensis	-60,737062	-38,323129				Varela et al. 2017

Continuação...

Neosclerocalyptus paskoensis	-61,683333	-38,566667				Varela et al. 2017
Neosclerocalyptus paskoensis	-60,076389	-37,134444				Varela et al. 2017
Neosclerocalyptus paskoensis	-64,295311	-36,622303				Varela et al. 2017
Neosclerocalyptus paskoensis	-65,276241	-26,11122				Varela et al. 2017
Neosclerocalyptus paskoensis	-56,306325	-34,706741	17620			Varela et al. 2017
Notiomastodon platensis	-73,103611	-40,57	15108	170		Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	15153		177	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	15153		912	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	14697		410	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	16092		368	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	14395		38	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	14427		317	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	12910		841	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	13188		129	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	13575		176	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	14185		278	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	32752		909	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	20610		2117	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-73,103611	-40,57	17537		1861	Gonzáles-Guarda et al. 2017
Notiomastodon platensis	-41,081211	-10,954819				Mothe et al. 2017
Notiomastodon platensis	-46,948583	-19,643389	61000		5000	Mothe et al. 2017
Notiomastodon platensis	-43,924461	-19,635103				Mothe et al. 2017
Notiomastodon platensis	-43,89	-19,626944				Mothe et al. 2017
Notiomastodon platensis	-80,918386	-2,222267	18000	1000		Mothe et al. 2017
Notiomastodon platensis	-80,918386	-2,222267	40500	500		Mothe et al. 2017
Notiomastodon platensis	-77,895833	-0,532222	6535		5885	Mothe et al. 2017
Notiomastodon platensis	-71,261944	-31,769167				Mothe et al. 2017
Notiomastodon platensis	-71,511389	-31,930278	10200		1200	Mothe et al. 2017
Notiomastodon platensis	-71,296389	-32615				Mothe et al. 2017
Notiomastodon platensis	-70,686667	-33,027778				Mothe et al. 2017
Notiomastodon platensis	-70,831667	-33,200556				Mothe et al. 2017
Notiomastodon platensis	-70,834444	-33,346667				Mothe et al. 2017

Continuação...

Notiomastodon platensis	-70,708611	-33,484444				Mothe et al. 2017
Notiomastodon platensis	-70,838611	-33,539444				Mothe et al. 2017
Notiomastodon platensis	-71,166389	-34,471667	10640	740		Mothe et al. 2017
Notiomastodon platensis	-71,540833	-34,314167				Mothe et al. 2017
Notiomastodon platensis	-72,136667	-36,626667				Mothe et al. 2017
Notiomastodon platensis	-73,173056	-38,718611				Mothe et al. 2017
Notiomastodon platensis	-72,197222	-39,574722				Mothe et al. 2017
Notiomastodon platensis	-72,926667	-40,557778	9800	8900		Mothe et al. 2017
Notiomastodon platensis	-72,876667	-40,9375	8650	7750		Mothe et al. 2017
Notiomastodon platensis	-73,205833	-41,503333	12700		1100	Mothe et al. 2017
Notiomastodon platensis	-69,859722	-11,180833				Mothe et al. 2017
Notiomastodon platensis	-69,859722	-11,180833				Mothe et al. 2017
Notiomastodon platensis	-59,808028	-37676				Mothe et al. 2017
Notiomastodon platensis	-59,808028	-37676				Mothe et al. 2017
Notiomastodon platensis	-61,89975	-35,810833				Mothe et al. 2017
Notiomastodon platensis	-57,550028	-35,071694				Mothe et al. 2017
Notiomastodon platensis	-60,92675	-31461				Mothe et al. 2017
Notiomastodon platensis	-59,199722	-38,283028				Mothe et al. 2017
Notiomastodon platensis	-59,199722	-38,283028				Mothe et al. 2017
Notiomastodon platensis	-60,697286	-31,610958				Mothe et al. 2017
Notiomastodon platensis	-60,25	-36,966667				Mothe et al. 2017
Notiomastodon platensis	-61,039556	-36,179111				Mothe et al. 2017
Notiomastodon platensis	-65,8	-28,016694				Mothe et al. 2017
Notiomastodon platensis	-58,466667	-37,116667				Mothe et al. 2017
Notiomastodon platensis	-58,017222	-34,905278				Mothe et al. 2017
Notiomastodon platensis	-60,740861	-31,629278				Mothe et al. 2017
Notiomastodon platensis	-60,740861	-31,629278				Mothe et al. 2017
Notiomastodon platensis	-58,630083	-34,761694				Mothe et al. 2017
Notiomastodon platensis	-60,21105	-33,333467				Mothe et al. 2017
Notiomastodon platensis	-60,102711	-34,062783				Mothe et al. 2017
Notiomastodon platensis	-58,522783	-34,853922				Mothe et al. 2017
Notiomastodon platensis	-58,647825	-34,576108				Mothe et al. 2017

Continuação...

Notiomastodon platensis	-57,542625	-38,005522			Mothe et al. 2017
Notiomastodon platensis	-57,542625	-38,005522			Mothe et al. 2017
Notiomastodon platensis	-59,428403	-34,654603			Mothe et al. 2017
Notiomastodon platensis	-58,739614	-38,554583			Mothe et al. 2017
Notiomastodon platensis	-58,463556	-34,3735			Mothe et al. 2017
Notiomastodon platensis	-58,463556	-34,3735			Mothe et al. 2017
Notiomastodon platensis	-58,423297	-34,571153			Mothe et al. 2017
Notiomastodon platensis	-60,073617	-38,851853			Mothe et al. 2017
Notiomastodon platensis	-57,948781	-34,913392			Mothe et al. 2017
Notiomastodon platensis	-57,897747	-34,862672			Mothe et al. 2017
Notiomastodon platensis	-60,375625	-36,971031			Mothe et al. 2017
Notiomastodon platensis	-57,406378	-35,641542			Mothe et al. 2017
Notiomastodon platensis	-58,459467	-34,561139			Mothe et al. 2017
Notiomastodon platensis	-60,511503	-31,741344			Mothe et al. 2017
Notiomastodon platensis	-60,483644	-31,756972			Mothe et al. 2017
Notiomastodon platensis	-60,495647	-31,774667			Mothe et al. 2017
Notiomastodon platensis	-60,547231	-33,092458			Mothe et al. 2017
Notiomastodon platensis	-60,547231	-33,092458			Mothe et al. 2017
Notiomastodon platensis	-60,547231	-33,092458			Mothe et al. 2017
Notiomastodon platensis	-60,547231	-33,092458			Mothe et al. 2017
Notiomastodon platensis	-60,547231	-33,092458			Mothe et al. 2017
Notiomastodon platensis	-60,547231	-33,092458			Mothe et al. 2017
Notiomastodon platensis	-64,264167	-27,783372			Mothe et al. 2017
Notiomastodon platensis	-57,621417	-32,158694	11500	500	Mothe et al. 2017
Notiomastodon platensis	-58,071389	-33,543056			Mothe et al. 2017
Notiomastodon platensis	-58,317861	-33514			Mothe et al. 2017
Notiomastodon platensis	-74,886111	-15,352778			Mothe et al. 2017
Notiomastodon platensis	-76,781497	-11,472525			Mothe et al. 2017
Pampatherium typus	-59,109167	-38,211389			Varela et al. 2017
Pampatherium typum	-58,233333	-38,433333			Varela et al. 2017
Pampatherium typum	-58,718611	-35,7225			Varela et al. 2017
Pampatherium typum	-58,67058	-26,623531	58000		Varela et al. 2017

Continuação...

Pampatherium typum	-56,866444	-29,672381	14925	Varela et al. 2017
Pampatherium typum		-29,671958		Varela et al. 2017

Supplementary Table 2 - Species and ranges modeled according to the range of occurrence

Espécie	Intervalo temporal(ka)	Intervalo modelado(ka)	Referências	Observação
Catonyx chilensis	44 a 8	23 a 8	Coltori et al. 2007 (Last Glacial mammals in South America: a new scenario from the Tarija Basin (Bolivia) / Ferrero 2008 (Scelidodon Ameghino (Tardigrada: Scelidotheriinae) en la Formación Tezanos Pinto (Pleistoceno tardío) de la provincia de Entre Ríos, Argentina)	Datação de camadas e/ou sedimentação
Catonyx cuvieri	42 a 11	23 a 11	Lopes e Pereira 2010 (Fossils of Scelidotheriinae Ameghino, 1904 (Xenarthra, Pilosa) in the Pleistocene deposits of Rio Grande do Sul, Brazil) / Auler et al. 2006 (U-series dating and taphonomy of Quaternary vertebrates from Brazilian caves)	Datação fóssil
Doedicurus clavicaudatus	30 a 6	23 a 6	Fariña et al 2014 (Arroyo del Vizcaíno, Uruguay: a fossil-rich 30-ka-old megafaunal locality with cut-marked bones) / Politis et al 2019 (Campo Laborde: A Late Pleistocene giant ground sloth kill and butchering site in the Pampas)	Datação fóssil
Eremotherium laurillardi	48 a 8	23 a 8	Lima-Ribeiro 2013 (Mudanças climáticas, colonização humana e a extinção da megafauna na América do Sul - Doutorado)	Datação fóssil
Glossotherium robustum	42 a 11	23 a 11	Pitana et al 2013 (Cranial and dental studies of Glossotherium robustum (Owen, 1842) (Xenarthra: Pilosa: Mylodontidae) from the Pleistocene of southern Brazil)	Datação fóssil
Glyptodon clavipes	58 a 10	23 a 10	Zurita et al 2009 (Paleontología del Chaco Oriental. Una nueva localidad con mamíferos fósiles pleistocenos en el río Bermejo (Formosa, Argentina)) / Kerber et al 2014 (Late Pleistocene vertebrates from Touro Passo Creek (Touro Passo Formation), southern Brazil: a review)	Datação de camadas e/ou sedimentação
Holmesina occidentalis	41 a 13	23 a 13	Czaplewski, Rincón e Morgan 2005 (Fossil Bat (Mammalia: Chiroptera) Remains from Inciarte Tar Pit,Sierra de Perijá, Venezuela) / Pujos e Sala 2004 (A systematic reassessment and paleogeographic review of fossil Xenarthra from Peru)	Datação fóssil / datação sítio

Continuação...				
Holmesina paulacoutoi	52 a 11	23 a 11	Francia, Zurita e Carlini 2015 (How Marine Isotope Stage 3 (MIS3) is reflected in northern Mesopotamia faunal assemblage of Argentina: The Xenarthra Cingulata case) / Keber et al 2014 (Late Pleistocene vertebrates from Touro Passo Creek (Touro Passo Formation), southern Brazil: a review)	Datação sítio/ datação sítio
Lestodon armatus	120 a 10	23 a 10	Brunetto et al 2015 (Late Pleistocene lithostratigraphy and sequences in the southwestern Mesopotamia (Argentina): Evidences of the last interglacial stage) / Martínez, Gutierrez e Tonni 2013 (Paleoenvironments and faunal extinctions: Analysis of the archaeological assemblages at the Paso Otero locality (Argentina) during the Late Pleistocene–Early Holocene)	Datação do sítio
Megatherium americanum	58 a 6	23 a 6	Zurita et al 2009 (Paleontología del Chaco Oriental. Una nueva localidad con mamíferos fósiles pleistocenos en el río Bermejo (Formosa, Argentina)) / Coltori et al. 2007 (Last Glacial mammals in South America: a new scenario from the Tarija Basin (Bolivia)	Datação de camadas e/ou sedimentação
Mylodon darwinii	80 a 13	23 a 13	Brandoni, Ferreiro e Brunetto 2010 (Mylodon darwini Owen (Xenarthra, Mylodontinae) from the Late Pleistocene of Mesopotamia, Argentina, with remarks on individual variability, paleobiology, paleobiogeography, and paleoenvironment) / Alberdi, Menegaz e Prado 1987 (Formas terminales de Hippidion (Mammalia, Perissodactyla) de los yacimientos del Pleistoceno tardío-Holoceno de la Patagonia (Argentina y Chile))	Datação do sítio / datação do fóssil
Neosclerocalyptus paskoensis	58 a 8	23 a 8	Zurita et al 2009 (Paleontología del Chaco Oriental. Una nueva localidad con mamíferos fósiles pleistocenos en el río Bermejo (Formosa, Argentina)) / Zurita et al 2011 (Neosclerocalyptus spp. (Cingulata: Glyptodontidae: Hoplophorini): cranial morphology and palaeoenvironments along the changing Quaternary.)	Datação de camas e/ou sedimentos

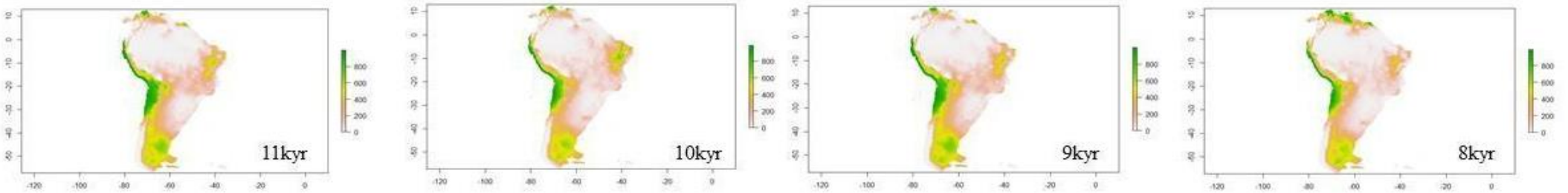
Continuação...				
Notiomastodon platensis	530 a 6	23 a 6	Dantas et al.2013 (A review of the time scale and potential geographic distribution of Notiomastodon platensis (Ameghino, 1888) in the late Pleistocene of South America)	Datação fóssil
Pampatherium typum	58 a 6	23 a 6	Zurita et al 2009 (Paleontología del Chaco Oriental: Una nueva localidad con mamíferos fósiles pleistocenos en el río Bermejo (Formosa, Argentina)) / Lopes 2009 (Alterações post mortem (pseudopaleopatologias) em fósseis de mamíferos pleistocênos do estado do Rio Grande do Sul, Brasil)	Datação de camadas e/ou sedimetos

Supplementary Table 3 - AUC values for the projections

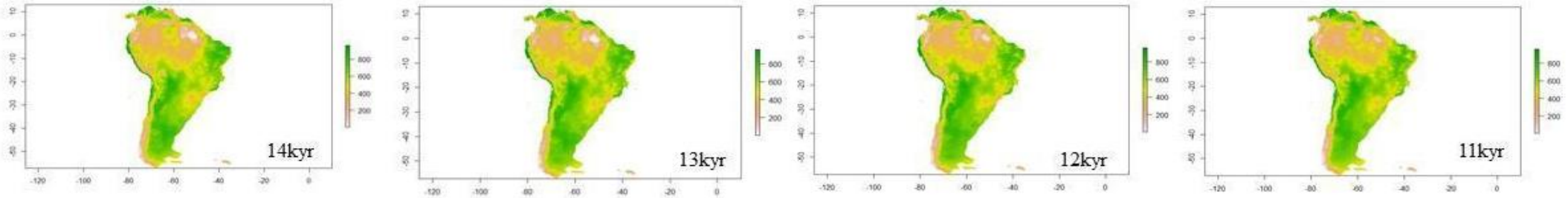
Espécies	**Número de instâncias**	**Média AUC's**
Catonyx chilenses (=*Scelidodon chilenses*)	14	0,929
Catonyx cuvieri	17	0,761
Doedicurus clavicaudatus	25	0,968
Eremotherium laurillardi	62	0,83
Glossotherium robustum	36	0,888
Glyptodon clavipes	38	0,922
Holmesina occidentalis	8	0,998
Holmesina paulacoutoi	10	0,811
Lestodon armatus	22	0,95
Megatherium americanum	39	0,909
Mylodon darwini	30	0,929
Neosclerocalyptus paskoensis	30	0,941
Notiomastodon platensis	112	0,919
Pampatherium typus	10	0,941

Supplementary Date 1 – Last modeled 4 ka

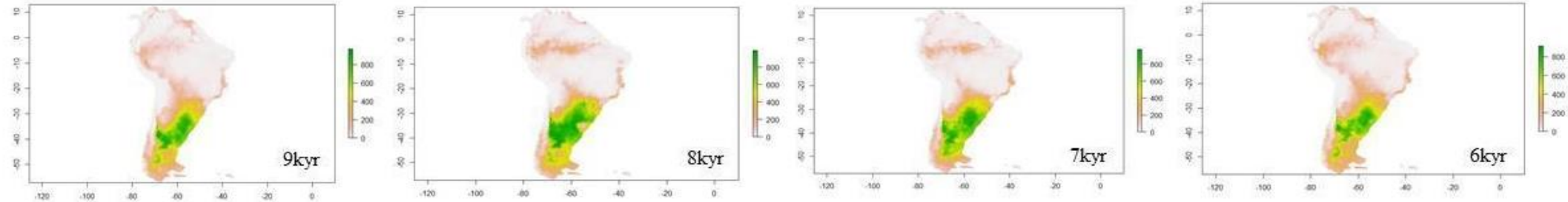
Catonyx chilensis



Catonyx cuvieri

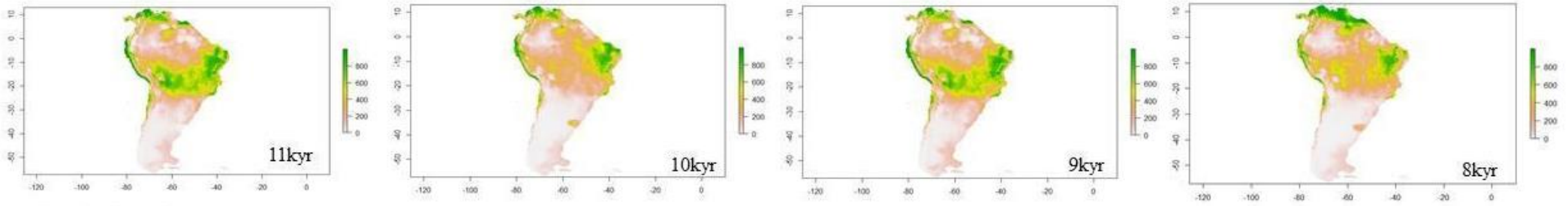


Doedicurus clavicaudatus

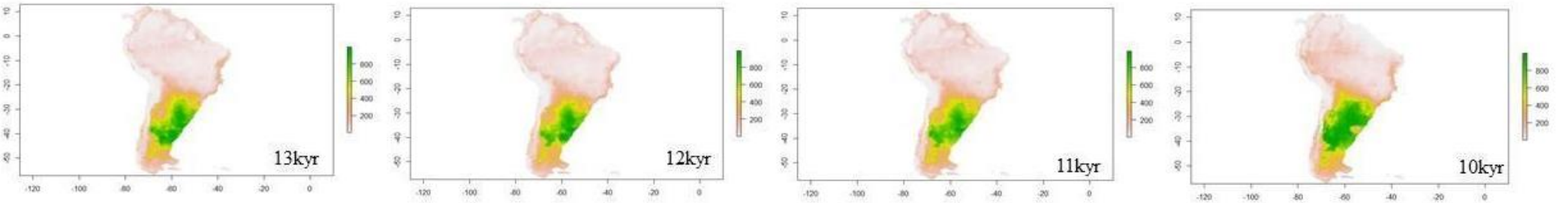


Continuação...

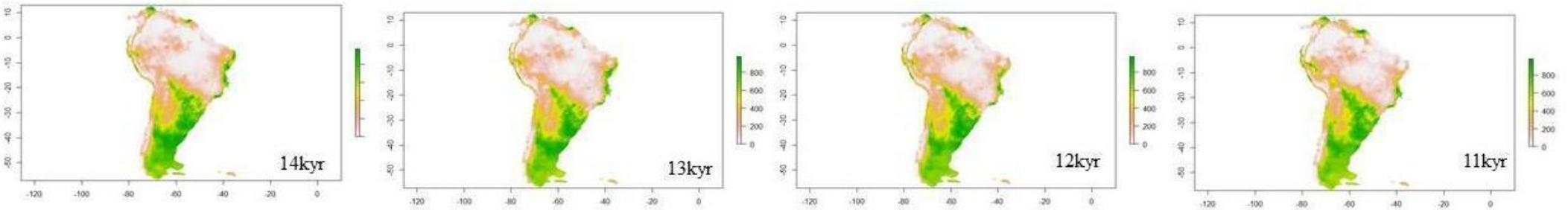
Eremotherium laurillardi



Glyptodon clavipes

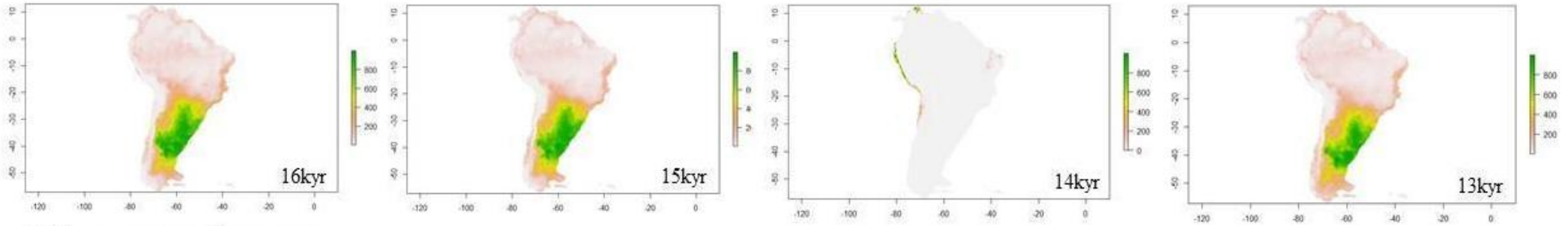


Glossotherium robustum

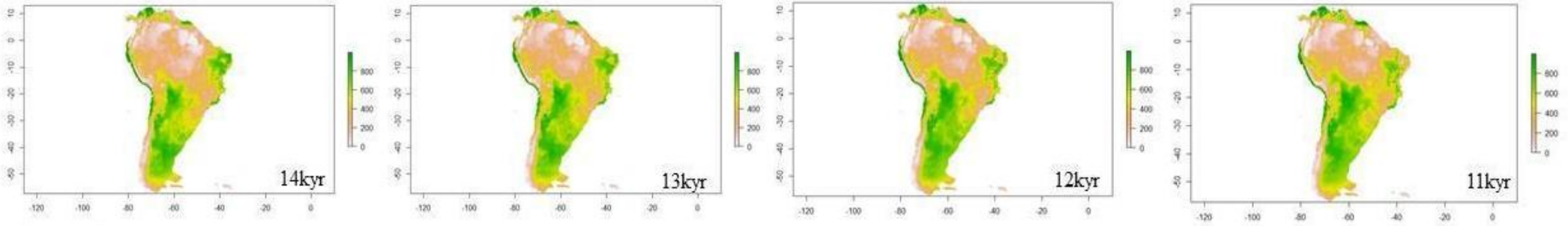


Continuação...

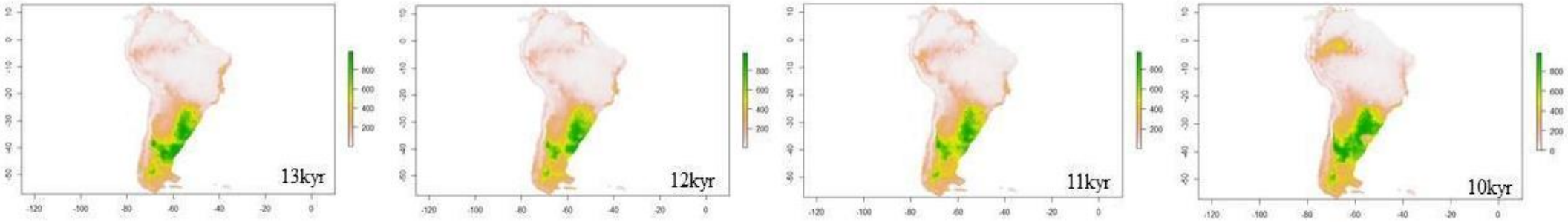
Holmesina occidentalis



Holmesina paulacoutoi

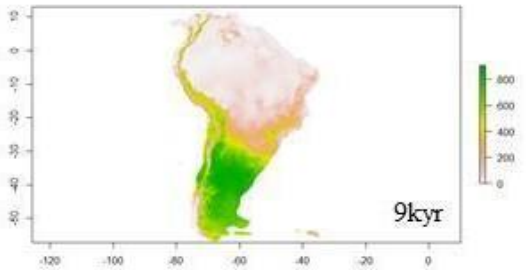


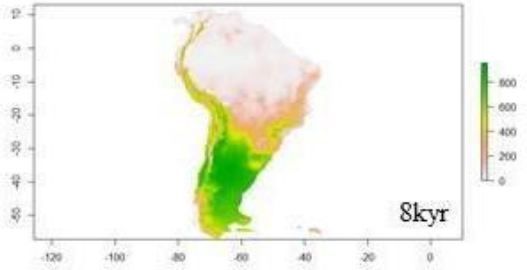
Lestodon armatus

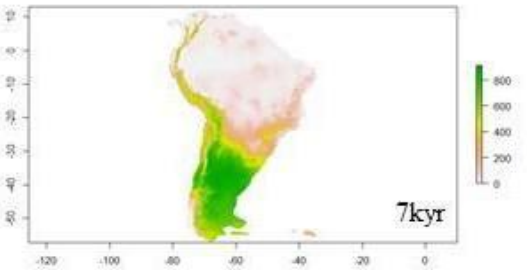


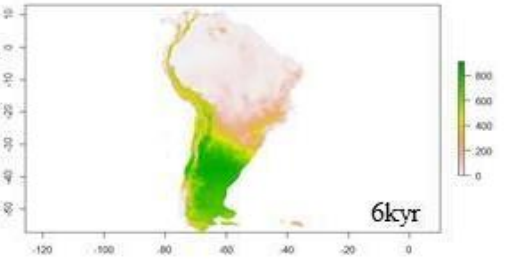
Continuação...

Megatherium americanum

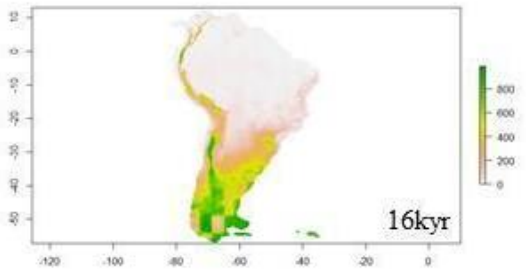


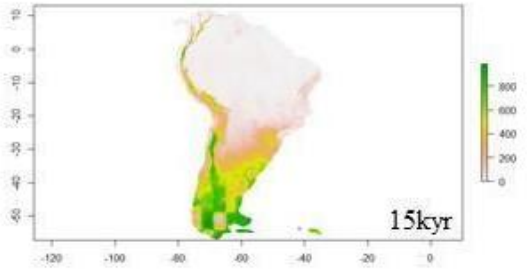


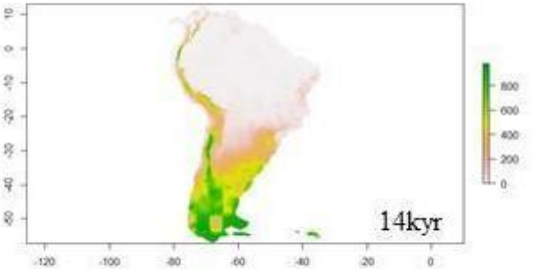


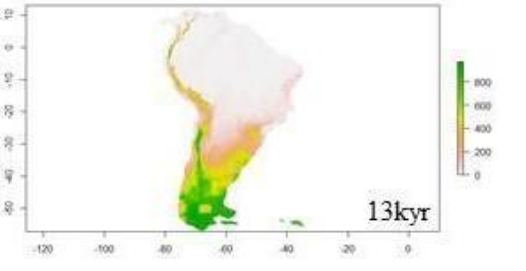


Milodon darwini

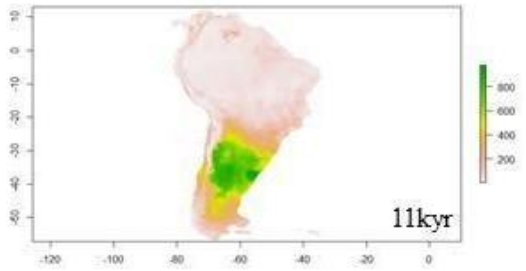


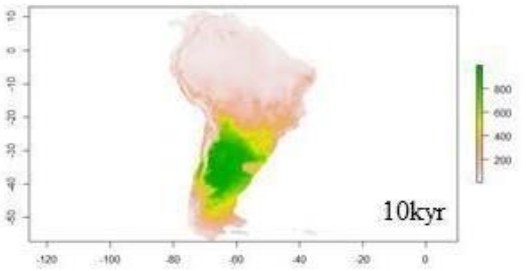


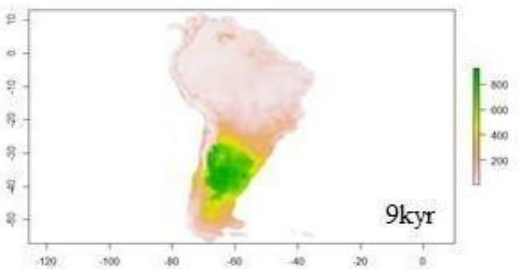


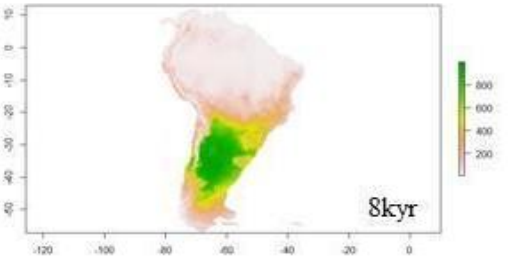


Neosclerocalyptus paskoensis



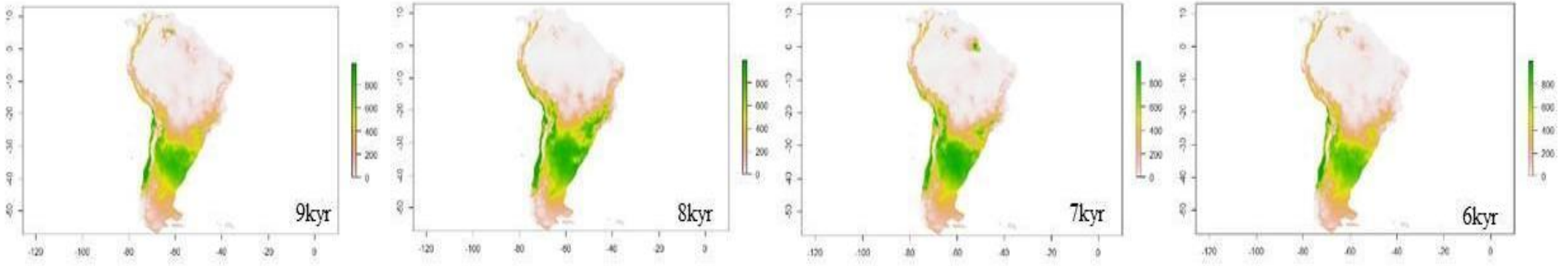




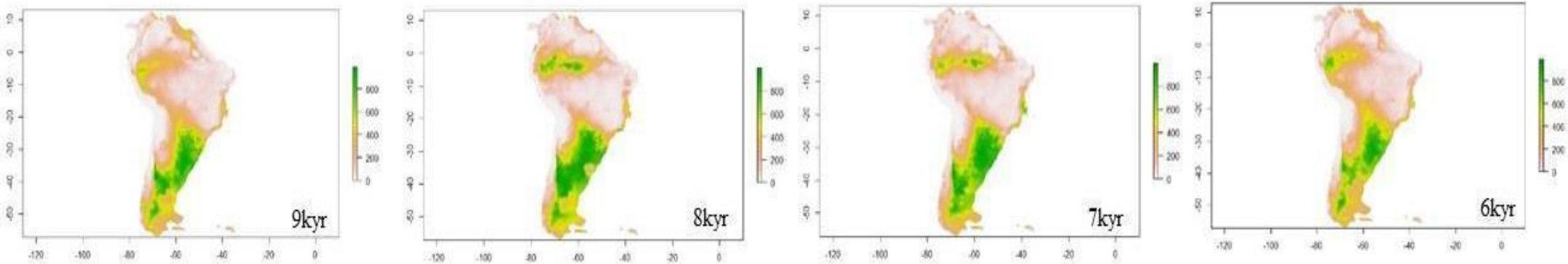


Continuação...

Notiomastodon platensis



Pampatherium typus



CAPÍTULO 3 – “Determinação de áreas prioritárias para prospecção de fósseis de herbívoros da megafauna quaternária”

Determinação de áreas prioritárias para prospecção de fósseis de herbívoros da megafauna quaternária

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RESUMO

Atualmente os trabalhos de prospecção fóssil são feitos em locais onde já se é conhecido por um bom potencial fossilífero e identificadas a partir dos históricos dessas localidades. Uma metodologia que auxilie na determinação de novas regiões fossilíferas otimizaria os trabalhos de campo, além de desenviesar as saídas a campo apenas a lugares com relatos prévios de ocorrências de fósseis, possibilitando assim a descoberta de novos sítios paleontológicos. O presente trabalho tem como objetivo determinar áreas com potencial fossilífero utilizando o *software Zonation* para indicar áreas prioritárias para busca de fósseis da megafauna. Nessa abordagem será avaliado o potencial do uso deste software, em duas etapas: (i) uma em escala continental, menos refinada, a partir dos mapas de potencial de distribuição modelados para as espécies extintas; (ii) outra em escala regional para áreas geográficas mais restritas, para as quais existam informações físicas, climáticas, geológicas e urbanas mais refinadas. O *Zonation* desenvolve um ranking prioritário de toda a paisagem classificando interativamente os locais, excluindo a unidade espacial que leva à menor perda agregada na biodiversidade. Foram utilizados mapas de adequabilidade de 14 espécies extintas da megafauna quaternária e mapas de índice de declive, população rural e presença de cavernas, com informações geográficas de maior resolução, para o Brasil. Os mapas de adequabilidade para as 14 espécies foram gerados no *Maxent* através de uma análise multitemporal, gerando projeções com intervalos temporais a cada mil anos, partindo de 23 ka até o registro datado mais recente de cada espécie. Na análise para o potencial fossilífero em escala continental, o mapa apresentou três grandes áreas principais com alto potencial fossilífero. São elas: (i) Nordeste do Brasil, (ii) região pampeana da Argentina, (iii) extremo norte do continente (Colômbia e Venezuela). Na análise regional, além de áreas já conhecidas, obtivemos resultados de possíveis novas áreas com potencial fossilífero, como a região central do estado de Sergipe. Podemos considerar o *Zonation* como uma metodologia altamente potencial para determinar áreas com prospecção de fósseis, mas faz-se necessário uma ampliação dos dados com um maior refinamento acrescentando mais mapas geomorfológicos e realização de saída de campo para testar e validar este *software*.

Palavras-chave: América do Sul; Análise multitemporal**;** Brasil; Fóssil; Mapas de adequabilidade; Paleontologia.

ABSTRACT

Currently, fossil prospecting works are carried out in places where it is already known for a good fossiliferous potential and identified from the histories of these locations. A methodology that assists in the determination of new fossiliferous regions would optimize field work, in addition to developing field trips only to places with previous reports of fossil occurrences, thus enabling the discovery of new paleontological sites. The present work aims to determine areas with fossiliferous potential using the Zonation software to indicate priority areas for searching for megafauna fossils. In this approach, the potential of using this software will be evaluated in two stages: (i) one on a continental scale, less refined, based on the distribution potential maps modeled for extinct species; (ii) another on a regional scale for more restricted geographic areas, for which there is more refined physical, climatic, geological and urban information. Zonation develops a priority ranking of the entire landscape interactively classifying the locations, excluding the spatial unit that leads to the lowest aggregate loss in biodiversity. Maps of suitability of 14 extinct species of the quaternary megafauna and maps of slope index, rural population and presence of caves were used, with geographic information of higher resolution, for Brazil. The suitability maps for the 14 species were generated in Maxent through a multitemporal analysis, generating projections with time intervals every thousand years, starting from 23 ka until the most recent dated record of each species. In the analysis for fossiliferous potential on a continental scale, the map presented three major main areas with high fossiliferous potential. They are: (i) Northeast Brazil, (ii) the Pampean region of Argentina, (iii) the far north of the continent (Colombia and Venezuela). In the regional analysis, in addition to already known areas, we obtained results from possible new areas with fossiliferous potential, such as the central region of the state of Sergipe. We can consider Zonation as a highly potential methodology to determine areas with prospecting for fossils, but it is necessary to expand the data with greater refinement by adding more geomorphological maps and carrying out fieldwork to test and validate this software.

Keywords: South America; Multitemporal analysis; Brazil; Fossil; Suitability maps; Palaeontology

1. Introdução

Ao longo da última década, muitos trabalhos vêm sendo desenvolvidos para identificar possíveis áreas de adequabilidade das espécies ou modelar seu nicho ecológico (Angeliere *et al.*,2016; Merow *et al*., 2013; Moreno e Lima-Ribeiro, 2015; Varela *et al*., 2011; Warren & Saifert, 2011; Iannella *et al.*,2019; Saunders *et al*., 2020). Alguns trabalhos usam esses mapas para determinar áreas de priorização de conservação de espécies atuais que apresentam riscos de extinção, entre outros fatores (Lehtomaki e Moilanen, 2013; Moilanen *et al*., 2011; Santangeli *et al*., 2019; Tognelli *et al*., 2011; Williams *et al*., 2012). Essas áreas compreendem regiões que foram identificadas como possíveis áreas de expansão de conservação de uma determinada espécie ou de um conjunto de espécies por apresentarem condições semelhantes a locais onde a espécie já habita. Essas regiões são determinadas com a finalidade de auxiliar na preservação diminuindo os riscos de extinção da mesma (Brum *et al*., 2017; Santangeli *et al*., 2019; Tognelli *et al*., 2011).

Além da conservação das espécies, algumas pesquisas utilizam esses mapas para determinar áreas apropriadas para conservação da diversidade biológica e para conservação de ecossistemas (Di Minin *et al*., 2013; Di Minin e Moilanen, 2012; Moilanen *et al*., 2008). Nesse sentido, o *Zonation* é um dos *softwares* empregados para tal análise, ao lado de outros como por exemplo, os algoritmos *C-plan* e *Marxan* (Kukkala e Moilanen, 2017). Até o presente momento, os trabalhos já publicados com esse intuito de identificar áreas prioritárias utilizaram apenas dados de espécies atuais (Brum *et al*., 2017; Santangeli *et al*., 2019; Tognelli *et al*., 2011) e não foram encontradas publicações onde tenham sido utilizados dados paleontológicos para o reconhecimento de áreas de alta diversidade no passado.

Atualmente os trabalhos de prospecção fóssil são feitos em locais já conhecidos por um bom potencial fossilífero e identificados a partir dos históricos dessas localidades. Antes de sair a campo é necessário fazer um planejamento completo, conhecer a área de estudo fazendo um levantamento bibliográfico do local e estudar o contexto geográfico da região, além de ser possível definir o tempo de prospecção e equipamentos necessários (Nobre e Carvalho, 2010). Uma metodologia que auxilie na determinação de regiões fossilíferas otimizaria os trabalhos de campo reduzindo o tempo utilizado para fazer os levantamentos dessas regiões em literaturas disponíveis, além de desenviesar as saídas a campo apenas em lugares onde já é conhecido com ocorrências de fósseis e possibilitando a descoberta de novos sítios paleontológicos.

O presente trabalho tem como objetivo determinar áreas com potencial fossilífero utilizando o *software Zonation* para indicar áreas prioritárias para busca de fósseis da megafauna. Nessa abordagem será avaliado o potencial do uso deste software, em duas etapas: (i) uma em escala continental, menos refinada, a partir dos mapas de potencial de distribuição modelados para as espécies extintas; (ii) outra em escala regional para áreas geográficas mais restritas, para as quais existam informações físicas, climáticas, geológicas e urbanas mais refinadas.

2. Localização e Grupo de Estudo

Megafauna é um grupo de mamíferos de grande porte com peso superior a 44 quilos (Hansen e Galetti, 2009). Esse grupo habitou todos os continentes (Fig.1) durante o Quaternário, com registros de ocorrências para algumas espécies até o Holoceno inicial (Barnosky *et al*., 2004; Doughty *et al*., 2016; Sandom *et al*., 2014; Stuart, 2015).

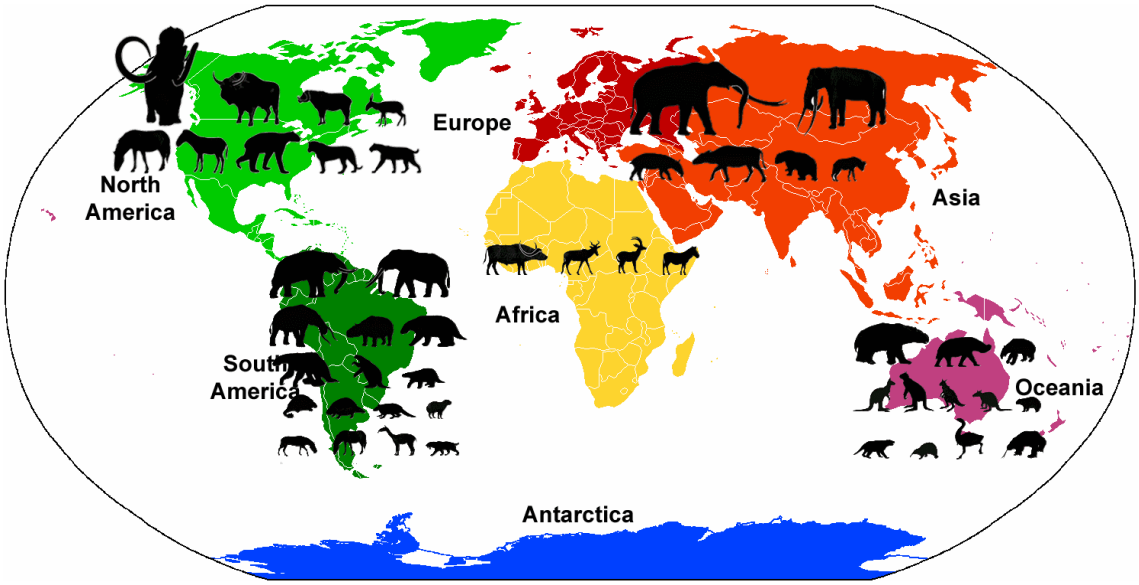

Fig.1. Principais grupos extintos da megafauna que habitaram os continentes. Adaptado de Stuart, 2015.

A América do Norte é um dos continentes que abrigava a maior diversidade desses grandes mamíferos. Estima-se que neste continente haviam cerca de 54 espécies divididas em grupos de mamutes (e.g *Mammuthus columbi*), bisões (e.g *Bison priscus*), preguiças (*Eremotherium laurillardi*) entre outros (Stuart, 2014). Calcula-se que a extinção no continente Norte Americano corresponde a aproximadamente 69% do total das espécies (Stuart, 2014).

A Eurásia, região formada pelos continentes Europa e Ásia, abrigava 48 espécies da megafauna e aproximadamente 17 delas foram extintas, divididas em grupos de rinocerontes-lanudos (e.g *Coelodonta antiquitatis*), elefantes (e.g *Palaeoloxodon antiquus*), hipopótamos (e.g *Hippopotamus amphibius*) e outros. A estimativa aproximada de extinção dessas espécies da Eurásia é de cerca de 37% com destaque para as espécies de elefantes, num total de três, que foram todas extintas (Stuart e Lister, 2012; Stuart, 2014).

A região da África subsaariana (exclui o norte do continente) ainda é rica em espécies da megafauna viventes desde o Pleistoceno. Estima-se que das 31 espécies apenas quatro espécies foram extintas: *Syncerus antiquus*, *Megalotragus priscus*, *Hippotragus leucophaeus*, *Equus capensis* que representam cerca de 13% do total (Stuart, 2014).

Para a Oceania não se sabe ao certo quantas espécies de megafauna que viveram desde o Pleistoceno foram extintas, devido às incertezas estratigráficas e problemas de datação direta (Stuart, 2014), mas estima-se que houve uma perda total dessas espécies há cerca de 46.000 anos (Roberts *et al*., 2001). Entre as espécies conhecidas extintas temos *Diprotodon optatum*, *Phascolonus gigas*, *Thylacoleo carnifex*, *Protemnodon brehus*, entre outros (Stuart, 2014 e Roberts *et al*., 2001).

O continente Sul Americano abrigou espécies da megafauna até o Holoceno inicial (Doughty *et al*., 2016). Durante a grande extinção do Pleistoceno tardio, estima-se que houve uma perda de cerca de 83% dessas espécies (Lima-Ribeiro e Diniz-Filho, 2013). Este continente foi habitado por uma grande variedade desses animais dos grupos de herbívoros e carnívoros, distribuídos principalmente entre os gêneros *Glossotherium, Lestodon, Mylodon, Scelidotherium, Eremotherium, Megatherium, Pampatherium, Glyptotherium, Glyptodon, Hoplophorus, Panochthus, Parapanochthus, Cuvieronius, Notiomastodon, Equus, Hippidion, Hemiauchenia, Palaeolama, Macrauchenia, Arctotherium, Smilodon* e *Protocyon* (Gallo *et al.*, 2013; Lima-Ribeiro e Diniz-Filho, 2013; Dantas e Cozzuol, 2016; Varella *et al.*, 2017). Na América do Sul algumas espécies das ordens Astrapotheria, Carnívora, Litopterna, Notoungulata, Proboscídea, Pyrotheriae, Xenungulata são endêmicas da América do Sul, ou seja são espécies exclusivas desse continente, como por exemplo, *Macrauchenia patachonica*,

Notiomastodon platensis, *Smilodon populator* e *Toxodon platensis* (Lucas, 2013; Buckley, 2015; Manzuetti *et al.*, 2018).

A América do Sul possui regiões com muitos estudos desenvolvidos sobre megafauna, principalmente em países como Bolívia em sítios como Valle de Tarija (Coltorti *et al*., 2010; Mothé *et al*., 2017; Tonni *et al*.,2009; Zurita *et al*., 2009; Zamorano e Oliva, 2020); Paso Otero, na Argentina (Prado *et al*., 2015; Martínez *et al*., 2012; Borrero, 2009; Scanferla *et al*., 2013; Cione *et al*., 2009); Formação Sopas no Uruguai (Pitana e Ribeiro, 2007; Ubilla, 2004; Ubilla *et al*., 2004; Oliveira e Pereira, 2009; Scherer *et al*., 2009). O Brasil é um país com grande potencial fossilífero. Vale destacar a Região Intertropical Brasileira (RIB) onde há uma grande quantidade de estudos que trabalham com os fósseis dessa região (Dantas, 2012; Dantas *et al*., 2013; Dantas, 2017; França *et al*., 2014 (a) França *et al*., 2014 (b); Araujo-Junior *et al*., 2013).

A Região Intertropical Brasileira (RIB) foi definida por Cartelle, 1999 como uma região zoogeográfica formada pelos estados do Nordeste (exceto Maranhão) juntamente com Goiás e os estados do Sudeste (exceto São Paulo) e com base na ocorrência de espécies de herbívoros e carnívoros com registros nesses estados, que são comumente encontrados em tanques e cavernas (Dantas e Cozzuol, 2016). Sergipe é um dos estados que compreende a RIB. Neste estado, além de uma grande variedade de grupos fósseis de invertebrados marinhos do Período Cretáceo (Bengtson *et al*., 2018; Franco-Neto, 2018; Manso e Souza-lima, 2012), há um diverso registro de vertebrados da megafauna, que viveram durante o Quaternário e eram mais comuns no Pleistoceno. Graças a esforços recentes de prospecção e coleta o número de espécies registradas para o Quaternário, no estado, apresentou um incremento, especialmente em regiões com a presença de tanques e cavernas naturais (Dantas, 2009; França *et al*., 2011) (Fig.2).

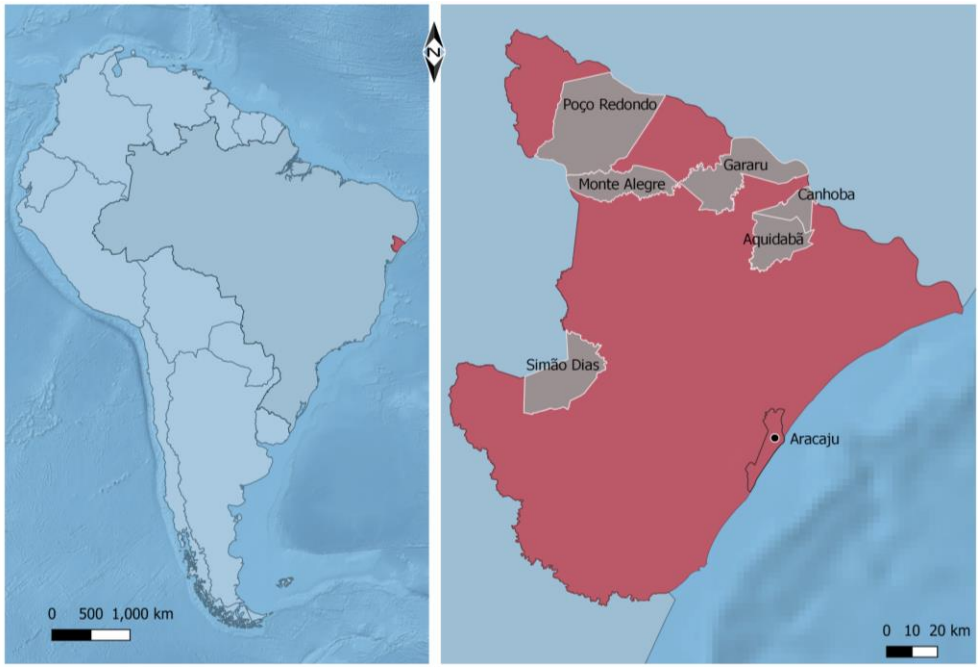

Fig.2. Mapa de Sergipe com destaque para os municípios onde há registros de fósseis da megafauna. Em cinza os municípios com registros fósseis da megafauna Quaternária. O município de Simão Dias apresenta fósseis encontrados em caverna e os outros municípios apresentam fósseis coletados em tanques naturais. Fonte: Modificado de base cartográfica da SEMARH.

As descobertas fósseis da megafauna quaternária em Sergipe tiveram início em 1884, com ocorrência predominantemente em afloramentos do tipo tanque (França *et al*., 2014a) e possui uma maior diversidade de espécies herbívoras. Do grupo dos herbívoros atualmente há registros de ocorrências fósseis das espécies *Catonyx cuvieri*, *Equus neogeus*, *Eremotherium laurillardi*, *Notiomastodon platensis*, *Pachyarmatherium brasiliense*, *Paleolama major*, *Toxodon platensis*, além de registros indeterminados de *Glyptotherium* e *Mylodontinae*. No

grupo dos carnívoros a única espécie com ocorrência para Sergipe é do dente de sabre *Smilodon populator* (Dantas e Cozzuol, 2016).

3. Métodos

3.1 Software Zonation

O *Zonation* é um *software* que desenvolve um ranking prioritário de toda a paisagem, em seguida, classifica interativamente os locais, excluindo a unidade espacial que leva à menor perda agregada na biodiversidade. Neste processo, chamado de meta-algoritmo do *Zonation*, os locais menos úteis são classificados como de menor prioridade (perto de 0) e as áreas de maior prioridade para a biodiversidade recebem as classificações mais altas (perto de 1) (Lehtomäki e Moilanen, 2013). Este *software* utiliza um conjunto de informações (*input*) necessárias para sua execução, por exemplo, mapas (formato TIFF) com modelos de distribuição das espécies estudadas e alguns parâmetros como pesos, serviços ecossistêmicos e conectividade e a partir desses dados ele gera um mapa com áreas quentes indicando que seriam áreas prioritárias.

O *Zonation* (versão 4.0) foi o *software* utilizado no presente trabalho para determinar as áreas prioritárias para prospecção e de acordo com Di Minin *et al*. (2014) são necessários três tipos de arquivos obrigatórios em todas as análises, que são:

I - Arquivo de projeto (formato .bat) criado em qualquer editor de texto e que deve especificar os arquivos de entrada e os arquivos de saída;

II - Uma lista de recursos de biodiversidade, arquivo de texto que pode ser criado no bloco de notas;

III - Um arquivo de configurações de execução (formato .dat) que define os recursos analíticos que serão usados na classificação de prioridade.

Com esse conjunto de arquivos para execução do *Zonation*, obtêm-se arquivos *outputs* com mapas indicando melhores áreas para conservação das espécies estudadas (Kukkala e Moilanen, 2017; Lehtomäki e Moilanen, 2013; Tognelli *et al*., 2011; Williams *et al*., 2012), que são as denominadas "áreas quentes do mapa" e gráficos com conjunto de curvas de desempenho indicando o limite onde cada recurso é retido na solução de conservação se diferentes frações da paisagem forem alocadas para conservação (Moilanen *et al*., 2011). A fig.3 resume os estágios das análises no *software Zonation.*

Foram feitas duas análises considerando escalas geográficas distintas: uma análise em escala continental, considerando toda a América do sul e outra em escala regional, onde informações geográficas referentes ao território brasileiro foram incluídas.

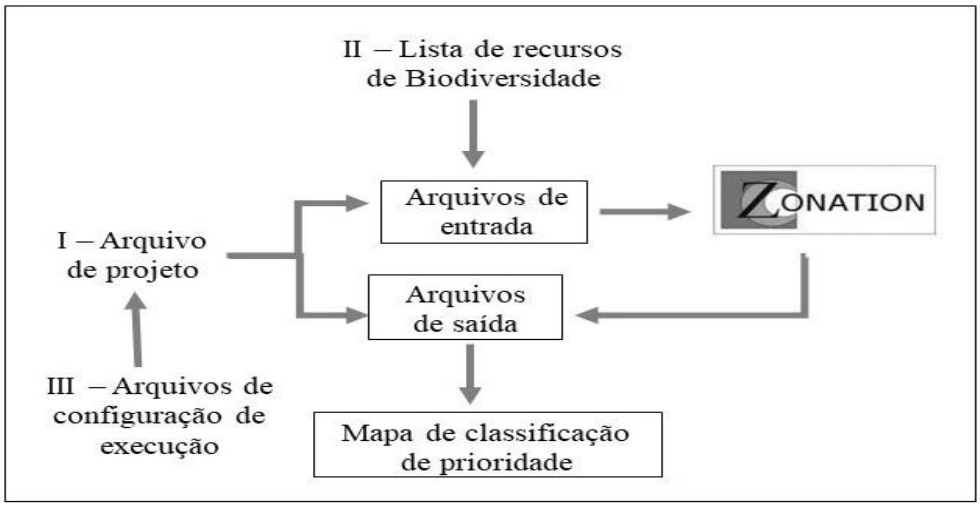

Fig.3. Resumo dos estágios de análises executadas no *Zonation* de acordo com Di Minin *et al*. (2014).

3.2 Análise em escala continental

Para a primeira análise foram utilizados mapas resultantes da modelagem de nicho ecológico de 14 espécies extintas, da megafauna quaternária sul americana. Foram incluídas as seguintes espécies: *Catonyx chiliensis*, *Catonyx cuvieri*, *Doedicurus clavicaudatus*, *Eremotherium laurillardi*, *Glossotherium robustum*, *Glyptodon clavipes*, *Holmesina occidentalis*, *Holmesina paulacoutoi*, *Lestodon armatus*, *Megatherium americanum*, *Mylodon darwini*, *Neosclerocalyptus paskoensis*, *Notiomastodon platensis* e *Pampatherium typus.*

A modelagem de nicho de cada espécie focal foi realizada previamente utilizando o *software Maxent* através de uma análise multitemporal, onde dados de ocorrências datados foram utilizados para gerar projeções com intervalos temporais a cada mil anos, partindo de 23 ka até o registro datado mais recente de cada espécie (Aragão *et al*., *in preparation*) e para todo continente sul americano. As modelagens de mil em mil anos foram adotadas como áreas potenciais de ocorrências para cada espécie em dado intervalo temporal. Um mapa com as médias dos mapas do potencial de ocorrência foi determinado para cada espécie. Esses mapas médios unificados foram considerados como representativo das melhores áreas de adequabilidade de cada espécie.

As resoluções padronizadas para os mapas com as modelagens de nicho para a América do sul podem ser observadas na tabela 1 a seguir:

Tabela 1
Resoluções dos mapas das modelagens.

Longitude (x)	0,042º
Latitude (y)	0,042º
xmin.	-81,58º
xmax.	-34,03º
ymin.	-57,13º
ymax	12,99º

3.3 Análise em escala regional

A segunda análise, com o objetivo de refinar o mapa final gerado pelo *Zonation*, considerou o resultado obtido na primeira análise a fim de se delimitar uma região geográfica mais restrita com potencial para ocorrência de uma maior diversidade de animais da megafauna no passado, mais próxima possível do centro atual onde essa pesquisa foi desenvolvida. Essa escolha se deu pela possibilidade de se testar a predição do modelo realizando saídas de campo otimizadas logisticamente.

Para essa segunda análise foram utilizados mapas com informações geográficas de maior resolução do Brasil, tal como registros de cavernas obtido do Centro Nacional de Pesquisa e Conservação de Cavernas (CECAV); desníveis obtidos do banco de dados WorldClim e densidade rural retirado da *Socioeconomic Data and Applications Center* (SEDAC). Nessa etapa os mapas das espécies foram recortados para os limites do Brasil com o auxílio do *software R* usando a função *crop*, do pacote *raster*, de maneira que ficassem do mesmo tamanho dos demais mapas utilizados para refinar os resultados do *Zonation*. As resoluções padronizadas para esses mapas englobando toda região brasileira podem ser observadas na tabela 2. Seus limites foram definidos a partir do contorno do próprio mapa do Brasil (fonte extraída do IBGE). O mapa final foi gerado para o Brasil e em seguida foi feito um recorte para Sergipe

considerando os limites de -40° a -35° em longitude e -12° a -8° em latitude, mantendo a resolução de 0,042°, a fim de facilitar a visualização das melhores áreas potencialmente próximas ao nosso centro de pesquisas.

Tabela 2
Resoluções padronizadas englobando a região brasileira.

Longitude (x)	0,042º
Latitude (y)	0,042º
xmin.	-73,99º
xmax.	-34,03384º
ymin.	-33,76º
ymax	5,20º

Por fim, para comparar o padrão de distribuição observado no *Zonation* com as ocorrências que se tem registro, foi gerado um mapa com os pontos de ocorrências de todos os táxons estudados, a partir dos registros catalogados no *Paleobiology Database* (PBDB) e com filtrado restrito apenas para as ocorrências do Quaternário. Nessa etapa, foram baixadas todas as ocorrências das espécies, de maneira que foram plotados em um mapa único os pontos que indicam onde os fósseis foram encontrados. Desta forma, foi possível uma melhor visualização de áreas com maior predomínio de registros do grupo estudado.

3.4 Atribuição de pesos e interpretação dos mapas resultantes

Cada mapa teve peso específico atribuído (entre 1 e 5) referente ao grau de influência na definição de áreas prioritárias para a prospecção. Peso 1 corresponde a variáveis menos influentes até peso 5, a mais influente, seguindo a metodologia de Di Minin *et al.*, (2014). Desta forma os mapas das espécies foram classificados com peso 3, mapa de cavernas peso 5 e peso 4 para os mapas de desníveis e densidade rural.

A definição das áreas consideradas como sugestivas para prospecção e potencialmente fossilífera, foi feita a partir da análise do padrão de cores "*Classic Zonation*" disponível nas configurações do programa, as áreas do mapa com as cores rosa, vermelho escuro e vermelho claro, dentro da área estudada.

4. Resultados e discussão

A fig. 4 representa de maneira mais detalhada as etapas de análises feitas pelo *Zonation* com os arquivos utilizados como dados de input e as configurações de execução e classificação para análise.

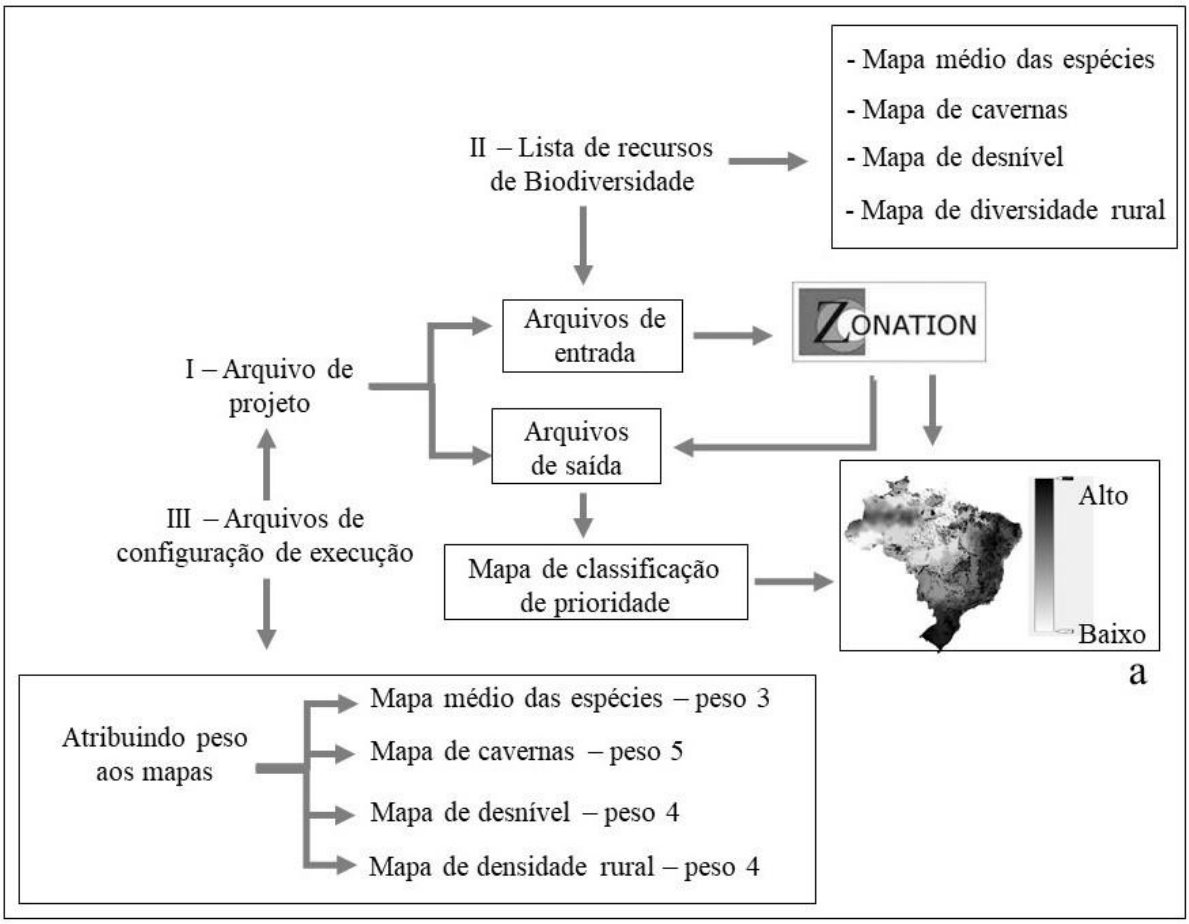

Fig.4. Fluxograma apresentando com mais detalhes as etapas de análises: Fase inicial contendo todos os arquivos de projeto (etapa I); arquivos utilizados como recursos de biodiversidade (etapa II); as configurações de execução e classificação de prioridade (etapa III); um exemplo de mapa de rank de priorização como resultado final (a) com um gradiente indicando que áreas com tons mais escuros (Alto) tem maior prioridade e áreas claras (Baixo) indicam áreas com menor prioridade.

4.1 Avaliação continental

A primeira análise feita a nível continental teve o objetivo de obter um aspecto geral de quais áreas o *Zonation* sugeriria com potencial fossilífero para a América do Sul utilizando apenas os mapas médios de adequabilidade da megafauna estudada. As áreas com cores mais próximas do vermelho claro, são as melhores regiões sugestivas como de grande potencial fossilífero (Fig. 3). Essas áreas indicariam regiões onde potencialmente poderíamos encontrar uma maior riqueza em termos de espécies fósseis herbívoras que poderiam ter co-ocorrido no passado. Observando o mapa pode-se verificar três principais áreas: (i) parte da região Nordeste do Brasil (Fig. 3a); (ii) região mais ao Sul do continente, compreendendo os países Uruguai e Argentina e Sul do Brasil (Fig. 3b); e (iii) a região mais noroeste do continente, na atual Venezuela/Colômbia (Fig. 3c). Esse resultado corrobora com trabalhos publicados que fizeram levantamentos de ocorrências na América do Sul e que confirmam a existência de abundância e riqueza de fósseis nessas três regiões (Domingo *et al*., 2012; Gallo *et al*., 2013; França *et al*., 2014b; Dantas *et al*., 2017).

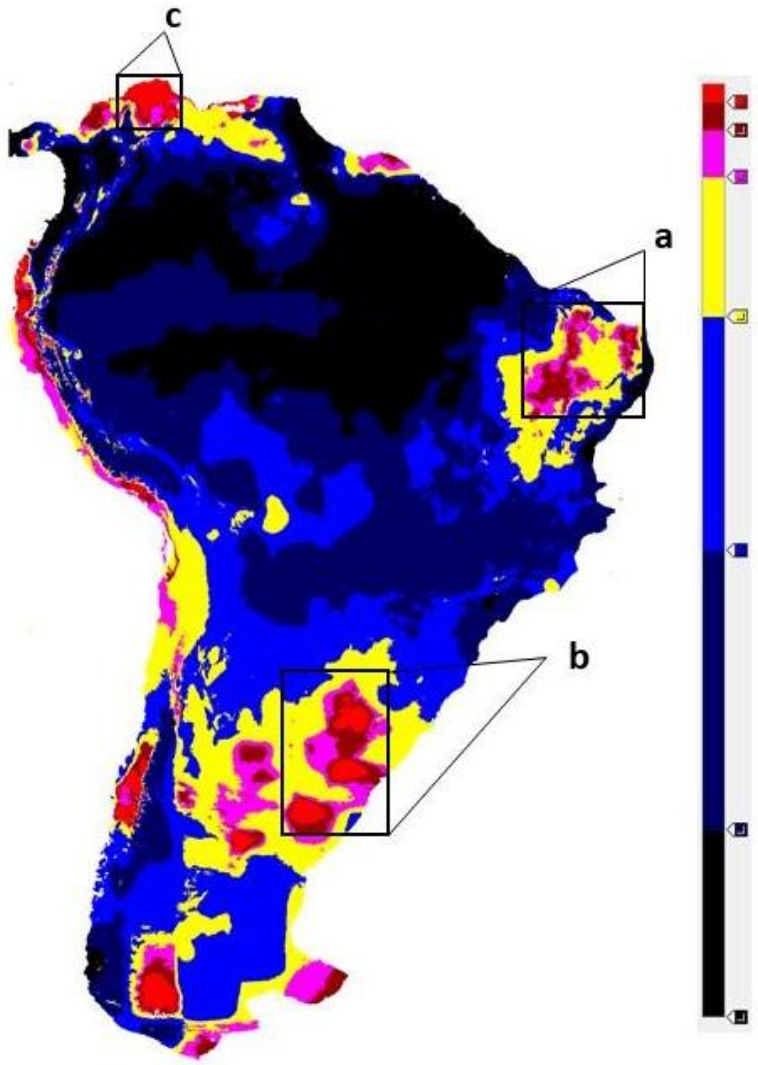

Fig.3. Mapa gerado pelo *software Zonation* para a América do Sul, considerando as 14 espécies listadas na seção Material e Métodos. A escala de cores indica que as áreas mais próximas da cor vermelho claro são as consideradas áreas quentes com maior probabilidade de ocorrência de fósseis e as áreas mais próximas da cor preta as áreas menos sugestivas. a- Nordeste do Brasil, b- Região Sul do continente compreendendo os países Uruguai e Argentina e Sul do Brasil, c- Região Noroeste do Continente.

Além das três áreas destacadas acima, na região mais ao Noroeste do continente, ocupando uma pequena área do Equador e do Peru, é possível identificar uma área vermelha indicando que também seria uma área com possibilidade de encontrar alta riqueza fossilífera. É conhecido na literatura trabalhos que estudam a megafauna nesses países como Ficarelli *et al*., 2003; Coltorti *et al*.,1998; Lindsay *et al*., 2020; Villavicencio e Werdelin, 2018; Rozas-Davila *et al*., 2016. O Chile também apresentou uma pequena região mais ao Sul do país, favorável para fósseis da megafauna e essa região coincide com o GT3 (*Generalized track*) proposto por Gallo *et al*., 2013. Neste trabalho, os autores estudaram registros de ocorrência de 27 espécies da megafauna com registros pela América do Sul e propõem trilhas generalizadas formadas a partir de vários registros de ocorrências que se sobrepõem (Fig .4). Além dessa área no Chile, as regiões **a** e **b** da figura 3 correspondem com os GTs 6 e 4 respectivamente, como é possível verificar na figura abaixo.

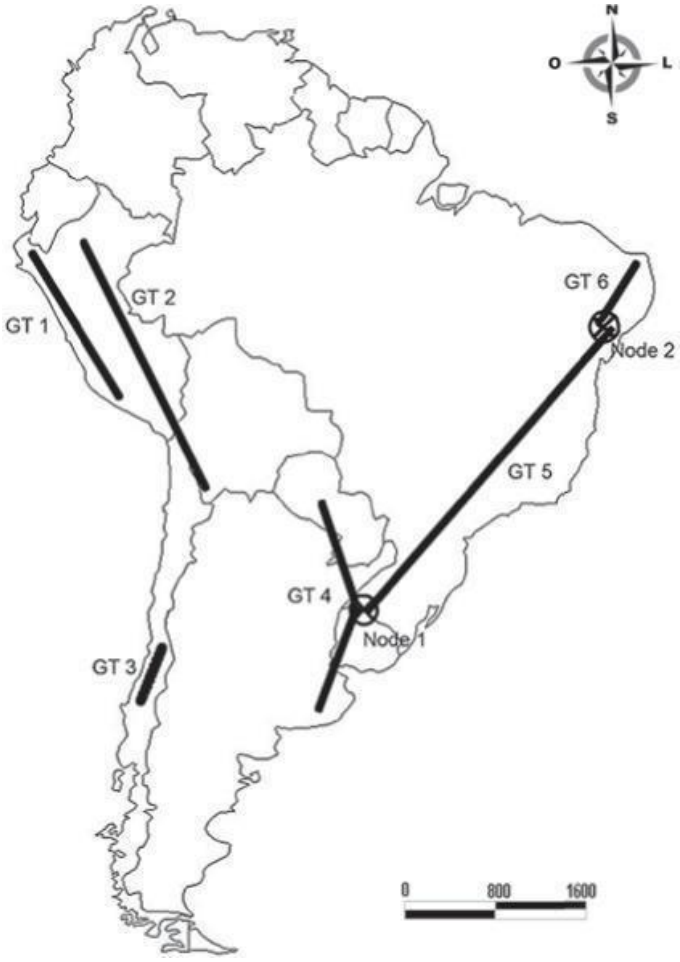

Fig.4. Trilhas e nós generalizados. GT3, GT4 e GT6 correspondem com algumas áreas resultantes. Fonte: Gallo *et al*., 2013.

Foi gerado um mapa no *Paleobiology Database* (PBDB) com pontos de ocorrências de todos os táxons estudados filtrados para o Quaternário, unificados em um mapa (Fig. 5), para comparar o padrão de distribuição observado neste mapa com o padrão obtido pelo *Zonation*.

Comparando os dois mapas, podemos observar que as áreas a e b da Figura 3, apresentam áreas semelhantes ao que pode ser observado nessas regiões correspondentes da Figura 5. Na Figura 5 é possível observar um "corredor" de ocorrências iniciando onde seria o Uruguai, passando pela Argentina e indo em direção ao Peru. Esse mesmo corredor é observado na Figura 3, mas com um padrão de cores diferentes e não apenas o vermelho menos intenso que indicaria que que toda a área seria potencialmente rica em fósseis, como as ocorrências registradas e observadas na Figura 5. O padrão das cores amarelo, rosa, vermelho escuro e vermelho claro estão presentes nesse corredor e na escala de cores do *Zonation* elas indicam que poderiam ser áreas com registro fóssil, amarelo e rosa apenas com menor possibilidade.

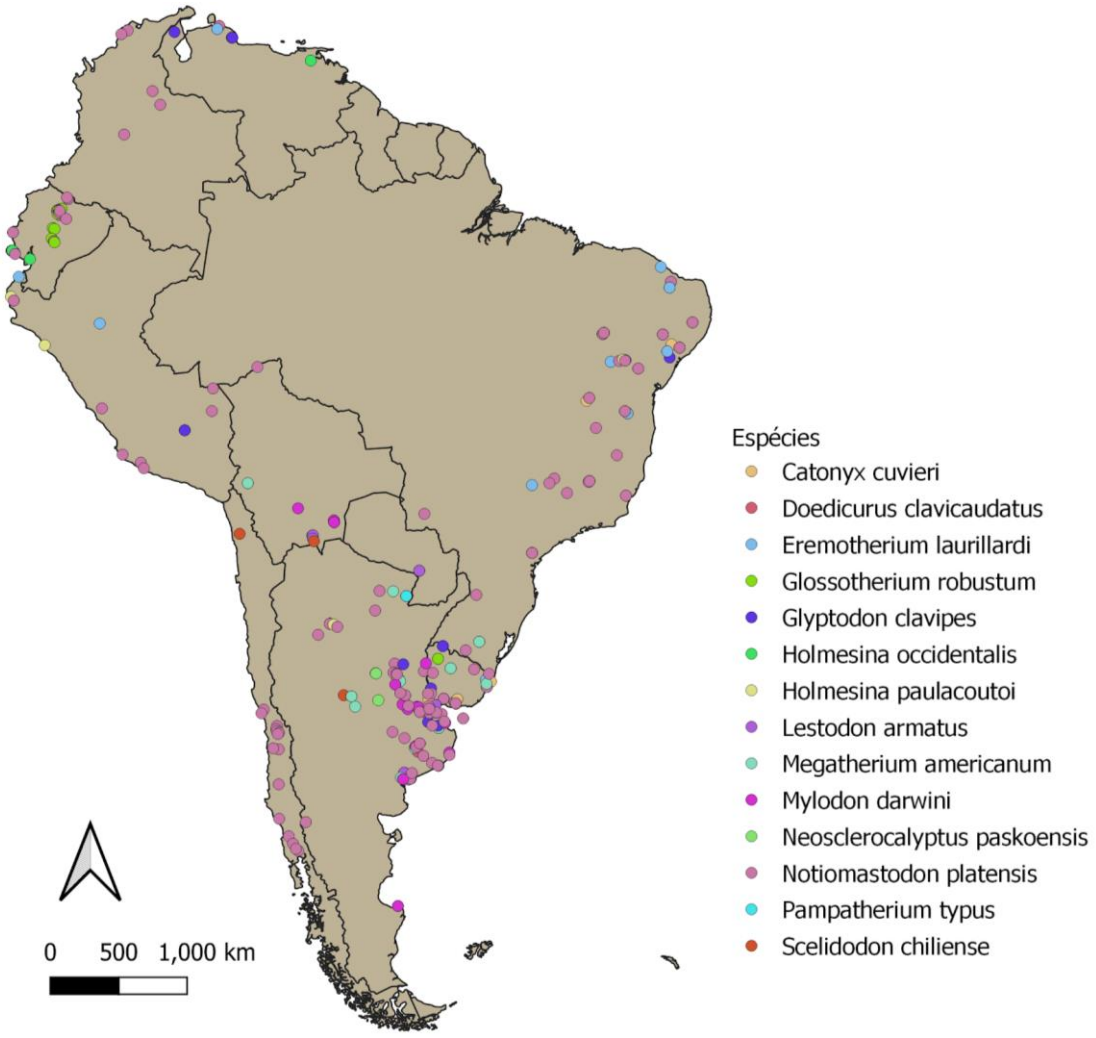

Fig.5. Mapa com todos os táxons estudados, de acordo com as ocorrências do *Paleobiology Database*. Link do PBDB onde foi feito o download das ocorrências fossilíferas para elaboração do mapa: https://paleobiodb.org/data1.2/occs/list.csv?base_name=Catonyx chiliensis, Catonyx cuvieri, Doedicurus clavicaudatus, Eremotherium laurillardi, Glossotherium robustum, Glyptodon clavipes, Holmesina occidentalis, Holmesina paulacoutoi, Lestodon armatus, Megatherium americanum, Mylodon darwini, Neosclerocalyptus paskoensis, Notiomastodon platensis, Pampatherium typus&show=coords,acconly - baixado em 24/10/2020.

O *Paleobiology Database* é um banco de dados alimentado de acordo com registros de ocorrência disponíveis na literatura, de maneira que a distribuição é apresentada com pontos representando os locais onde o fóssil foi encontrado. Já o *Zonation* apresenta as melhores áreas com um padrão de escalas de cores estimando uma área mais abrangente, diferente de locais exatos de ocorrência. Os mapas das espécies estudadas que foram utilizados no *Zonation*, não foram gerados apenas com as ocorrências das espécies, mas também dados climáticos do período estudado. O *Zonation* gerou um mapa apresentando um ranking estatístico de áreas que seriam favoráveis de acordo com as ocorrências e projeções de nicho climático, correspondendo a uma análise mais robusta do que apenas uma sobreposição dos registros de ocorrência.

No Brasil, a região da Amazônia também é uma área conhecida com ocorrência de fósseis da megafauna (Paula Couto, 1983; Rancy, 1991; Rossetti *et al*., 2004; Nascimento, 2008) e o mapa gerado não apontou a Amazônia como sendo uma área prioritária para busca de material fossilífero. Isso pode ser explicado pelo fato de que a maior parte das 14 espécies selecionadas para a modelagem não apresentaram a Amazônia como sendo uma área de alta adequabilidade para sua existência. Como o *Zonation* sobrepõem e prioriza as regiões mais adequadas para o

conjunto de todas as espécies consideradas, mesmo que algumas de fato ocorram na Amazônia, o programa só indicará as regiões onde potencialmente praticamente todas as espécies possam ocorrer conjuntamente. Esse resultado pode ser incrementado fazendo uma análise específica com espécies fósseis e mapas com características físicas, geográficas e sociais próprias da região amazônica, por exemplo.

O mapa do PBDB (Fig. 5), assim como o mapa gerado pelo *software*, não indicou que a região Amazônica é uma região onde há ocorrência dos fósseis selecionados para este estudo. Esse fato pode ser justificado por uma composição faunística distinta daquela escolhida para análise no presente trabalho.

4.2 Avaliação regional

Sergipe é um dos estados que compõem a região Nordeste do Brasil, com grande potencial fossilífero e foi a área selecionada para realizar a segunda análise. O resultado dessa análise foi considerado muito positivo, pois é possível observar no recorte do mapa que as áreas do Noroeste (Fig. 6a) e Oeste (Fig. 6b) do estado representadas principalmente pelos municípios de Poço Redondo e Simão Dias, respectivamente, são áreas sugestivas para prospecção de fósseis e esse resultado combina com os dados disponíveis na literatura (Dantas *et al*., 2005; Dantas, 2009; França *et al*., 2011; Dantas, 2010; Dantas, 2012).

A região Noroeste do estado resultante como área sugestiva (Fig. 5a) compreende os municípios de Canindé do São Francisco, Poço Redondo, Porto da Folha e Monte Alegre. Desses municípios há registros de megafauna apenas em tanques dos municípios de Poço Redondo e Monte Alegre. Esses registros são representados pelas espécies *Eremotherium laurillardi*, *Notiomastodon platensis*, *Catonyx cuvieri*, *Palaeolama major*, *Toxodon platensis*, *Smilodon populator* e *Pachyarmatherium* sp. (França *et al*., 2011). A área identificada como 6b é equivalente às regiões dos municípios de Simão Dias, Lagarto, São Domingos, Riachão do Dantas e Tobias Barreto. Dessa área, há registro de megafauna apenas em uma caverna em Simão Dias, onde foi encontrado fósseis de *Glyptodon clavipes* e de um roedor da espécie *Galea spixii*, mas este último não é considerado representante da megafauna (França *et al*., 2011). Sendo assim, não podemos considerar que a área 6b apresenta uma alta riqueza da megafauna, visto que há registros de apenas uma espécie e em uma localidade, diferente da área 5a onde há mais espécies, além de um maior número de localidades em cada município correspondente. O direcionamento de mais buscas para essa região seria encorajado, com potencial para achados fósseis de mais espécies.

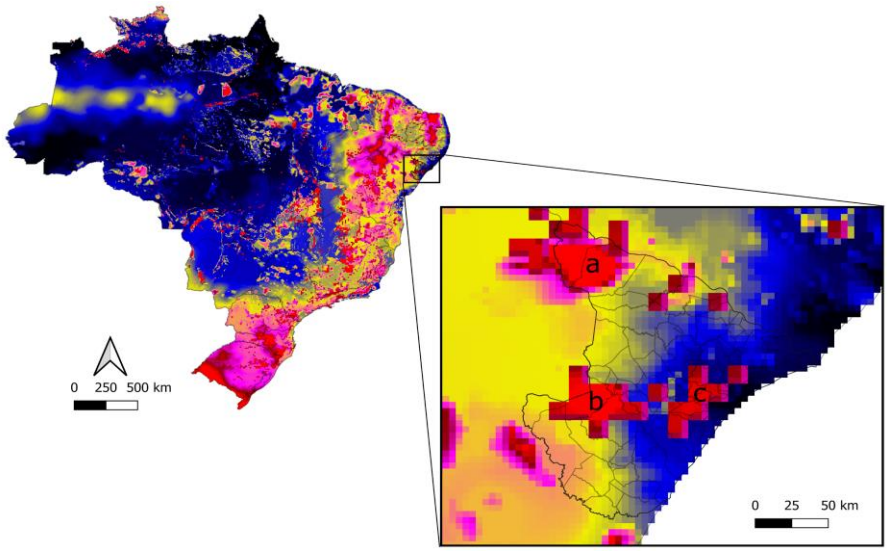

Fig.6. Recorte do mapa regional com destaque para o estado de Sergipe. As áreas com tons na cor vermelho vivo, são as áreas sugestivas para prospecção no estado. a- Região Noroeste, b- Região Oeste, c- Região Centro-Leste.

É importante destacar também a área compreendida pela região Centro-Leste de Sergipe (Fig. 6c) formada principalmente pelos municípios de Riachuelo, Laranjeiras, Maruim, Rosário do Catete e Nossa Senhora do Socorro e que resultou em uma área potencial para prospecção. Esses municípios são comumente conhecidos pela grande diversidade de animais invertebrados marinhos do período Cretáceo (Bengtson *et al*., 2018; Franco-Neto, 2018; Manso e Souza-lima, 2012), havendo apenas um registro de megafauna no município de Laranjeiras (Ver Omena *et al*., 2020).

Dessa forma, tal região seria sugestiva para prospecções futuras, como possível nova área com registros paleontológicos. Essa nova área pode ser utilizada como principal área para validar o uso deste *Software* e que faz parte das perspectivas futuras dessa pesquisa, bem como acréscimo de mapas geomorfológicos específicos para o estado.

Essa é uma região onde sabe-se que há muitas cavernas, catalogadas no Cadastro Nacional de Cavernas do Brasil. O município de Laranjeiras é o que apresenta um maior número de cavernas catalogadas (total de 15) esse seria um bom município para iniciar a busca por fósseis da megafauna nessa nova área sugerida pelo *Zonation*, considerando também o registro que é conhecido.

O recorte do mapa final foi feito para o estado de Sergipe por ser um estado conhecido como de grande potencial fossilífero e por ser uma região próxima de onde esse trabalho foi desenvolvido, facilitando o uso desse resultado para realização de saídas a campo em perspectivas futuras.

5. Conclusão

As duas análises propostas neste artigo apresentaram resultados positivos e consideráveis quando comparados com registros de ocorrências encontrados na literatura. Na primeira análise feita em escala continental, foram utilizados apenas mapas com áreas mais adequadas para as espécies estudadas, a fim de verificar esse primeiro resultado comparando com os trabalhos já publicados. Já na segunda análise feita em escala regional com maior atenção para o estado de Sergipe, além desses mapas das espécies, foram utilizados mapas geográficos do Brasil. Nesta última etapa o foco principal foram esses mapas geográficos com características que influenciam no encontro de possíveis áreas paleontológicas. Ao determinar quais áreas seriam sugestivas para prospecção de fósseis a partir do mapa gerado pelo *Zonation*, verificamos se são áreas já conhecidas com ocorrência de fóssil. Foi observado também sugestões com novas possíveis áreas para prospecção, nesse caso, foram analisadas características favoráveis para encontrar megafauna visto que é uma área com grande potencial paleontológico, mas não há na literatura registros desse grupo de grandes mamíferos para a região.

Vale destacar no resultado da escala continental, a região Amazônica que apesar de ser uma área com registros de megafauna, não foi sugerida no mapa final do *software*. Esse resultado pode ter sido influenciado pelos mapas médios utilizados, onde a maioria das espécies também não apresentaram essa área como adequada para sobrevivência, o que pode ser aperfeiçoado com o acréscimo de mais registros das espécies já estudadas, bem como acréscimo de outras espécies fósseis deste e de outros grupos extintos.

Na análise regional foi observado uma nova área com potencial fossilífero formada por municípios de Sergipe em que há poucos registros de megafauna (Fig. 6c). Nessa etapa de análise em que foram utilizados mapas geográficos do Brasil, um desses mapas foi o de ocorrência de cavernas no país. De acordo com o banco de dados do Cadastro Nacional de Cavernas do Brasil (CNC) há cavernas catalogadas nos municípios desse estado, o que pode ter influenciado o *Zonation* a determinar essa região como potencialmente fossilífera. Considerando que de modo geral há registros de megafauna também em cavernas, pode ser uma

boa área sugestiva para prospecção e verificar a possibilidade de ocorrência de novo afloramento paleontológico.

Diante dos resultados obtidos, podemos considerar o *Zonation* como uma metodologia de alto potencial para determinar áreas com prospecção de fósseis, visto que as áreas resultantes corroboram com as localidades já conhecidas em que há registros de fósseis. A incorporação de mapas com um maior refinamento de dados geomorfológicos do estado e a realização de saída de campo para testar e validar este *software* potencialmente enriquecedoras para a aplicação da metodologia proposta.

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CAPÍTULO 4 – CONCLUSÃO

Esse trabalho foi desenvolvido em duas propostas de estudo:

- (i) utilizando uma inovação metodológica para compreender de forma contínua a variação da paleodistribuição pela América do Sul das espécies *Catonyx cuvieri*, *Catonyx chilensis*, *Eremotherium laurillardi*, *Glossotherium robustum*, *Lestodon armatus*, *Megatheirum americanum*, *Mylodon darwini*, *Doedicurus clavicaudatus*, *Glyptodon clavipes*, *Holmesina occidentalis*, *Holmesina paulacoutoi*, *Neosclerocalyptus paskoensis*, *Pampatherium typus* e *Notiomastodon platensis*, representantes da megafauna do Quaternário, em períodos próximos ao seu último registro datado;
- (ii) através do uso dos mapas gerados na proposta anterior e mapas geográficos do Brasil, propor uma nova metodologia com o uso de um *software* para tentar prever áreas potenciais para prospecção de fósseis.

Nas duas propostas obtivemos resultados consideráveis positivos, mas também alguns aspectos negativos para serem analisados e corrigidos ou adaptados para melhores resultados em perspectivas futuras.

Na primeira proposta, as espécies apresentaram um padrão de distribuição independente, mas semelhante entre a maioria das espécies. Não foram observadas variações bruscas nesses padrões em nenhuma das espécies, bem como todas ainda apresentaram possíveis áreas adequadas no último mil ano modelado e que se tem registros de ocorrências das mesmas. Um aspecto que pode ser considerado negativo nessa proposta, foi a quantidade de espécies estudadas e o número de ocorrências utilizadas na construção dos mapas de adequabilidade. E esses resultados podem ter uma influência direta em parte dos resultados da segunda proposta.

A segunda proposta foi desenvolvida em duas etapas que se complementam. Na primeira etapa a análise foi feita a nível continental utilizando os mapas resultantes da proposta anterior e o *software Zonation* para tentar estimar áreas em que pode ser encontrado fósseis das espécies estudadas. O uso dos mapas da primeira proposta pode ser considerado um aspecto negativo da metodologia, visto que a maioria das espécies não apresentaram regiões adequadas em boa parte da região Norte do Brasil. Sabe-se que essa é uma área com ocorrências fossilíferas, mas o mapa final não apresentou essa área como uma boa área para para encontrar fósseis. A segunda etapa utilizou os mapas das espécies com recorte para o Brasil e mapas com registros de cavernas, densidade rural e declive, para refinar o resultado da primeira etapa e fazer uma análise a nível regional, para o estado de Sergipe. Os resultados obtidos como áreas

potenciais para prospecção, coincidem com as áreas onde já se sabe que apresentam afloramentos paleontológicos. Além de sugerir uma nova área até então desconhecida, em termos do seu potencial para prospecção fóssil. Um aspecto negativo pode ter sido a utilização de poucos mapas geográficos, de maneira que a utilização de mais informações geográficas pode melhorar os resultados dessas áreas sugestivas.

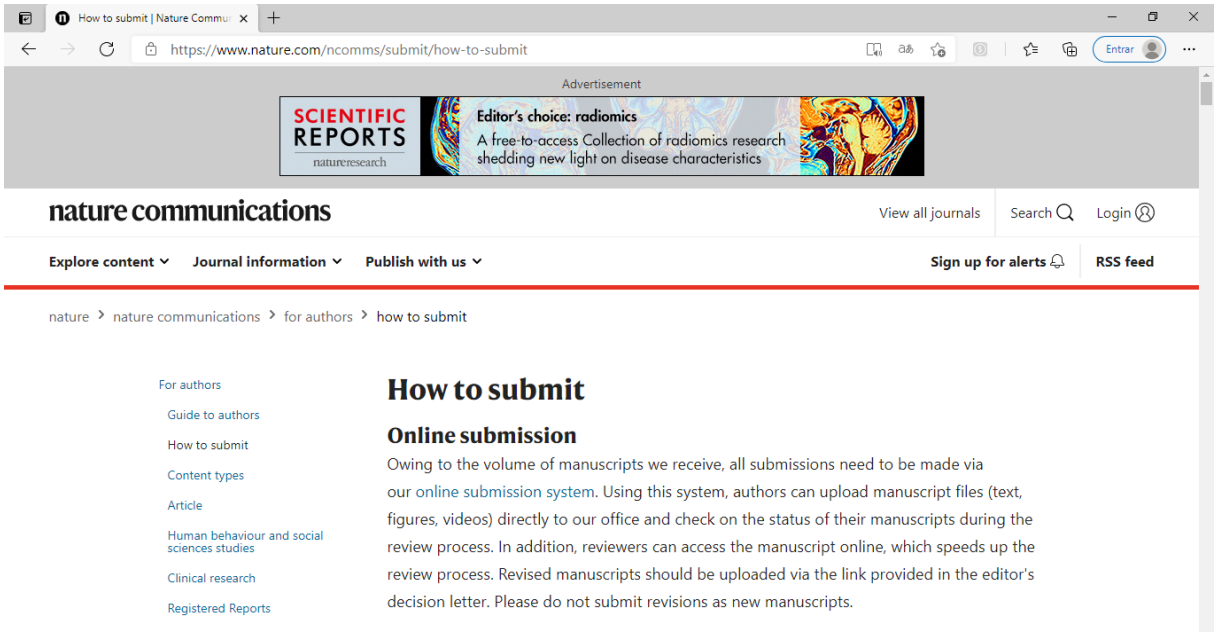
Sendo assim, podemos considerar que a metodologia de elaboração de mapas de adequabilidade com uso de camadas climáticas a cada mil anos e simulação das instâncias realizada na primeira proposta, como uma metodologia válida para determinar quais seriam as melhores áreas de sobrevivência e/ou adaptação das espécies estudadas, visto que os resultados apresentaram um padrão de distribuição semelhante ao que é encontrado na literatura, com exceção da espécie *Notiomastodon platensis.* O uso desses mapas para completar um conjunto de dados e arquivos de execução para o *Zonation* e juntamente com os mapas geográficos pode ser considerada como uma metodologia altamente potencial, já que as áreas geradas pelo software, correspondem aos locais já conhecidos como potencialmente fossilíferos.

Para obter melhores resultados do *Zonation* é necessário a realização de mais estudos considerando um número maior e mais diverso de espécies, registros de ocorrências e mais informações geomorfológicas da região, além da realização de saídas de campo para testar e validar a performance preditiva do programa. Essas são as principais propostas a serem desenvolvidas em perspectivas futuras.

ANEXOS

ANEXO 1 – NORMAS PARA SUBMISSÃO NAS REVISTAS

Artigo 1 - NATURE COMMUNICATIONS



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ANEXO 3 – JUSTIFICATIVA DOS COAUTORES

Pablo A. Martinez – Possui licenciatura em Genética pela Universidad Nacional Misiones (2007), Mestrado em Ecologia na UFRN (2010), e Doutorado em Ecologia na UFRN (2013). Têm trabalhado com diversas ferramentas como citogenética molecular, morfometria geométrica, filogeografia, analises comparativos, modelagem de nicho e análises espaciais. Está interessado em compreender como os processos históricos e ecológicos modulam as variações fenotípicas e a distribuição dos vertebrados (Texto lattes).
http://lattes.cnpq.br/5991773287291413

Contribuiu auxiliando no tratamento dos mapas modelados utilizados no capítulo 2 "Mapas de adequabilidade e padrões de distribuição de fósseis da megafauna Quaternária na América do Sul: uma nova abordagem metodológica" e dos mapas de geológicos utilizados no capítulo 3 "Determinação de áreas prioritárias para prospecção de fósseis de herbívoros da megafauna Quaternária".

Pablo Riul – Bacharel em Ciências Biológicas pela Universidade Federal da Paraíba (2004), Mestre em Ciências Biológicas (Zoologia) pela Universidade Federal da Paraíba (2007) e Doutor em Ecologia (2015) pela Universidade Federal de Santa Catarina (Doutorado sanduíche na Universidad Rey Juan Carlos, Madri, Espanha). Atualmente é professor Adjunto II do Departamento de Sistemática e Ecologia da UFPB onde coordena o Programa de Pós Graduação em Ecologia e Monitoramento ambiental (PPGEMA) do Campus IV. Tem experiência na área de Ecologia, com ênfase em Biodiversidade e Macroecologia de organismos costeiros, com interesses principalmente nos seguintes temas: Biodiversidade de comunidades associadas a bancos de rodolitos e distribuição de organismos marinhos da zona costeira.
http://lattes.cnpq.br/4057417762152773

Auxiliou no uso do *Zonation* e nas dúvidas sobre as funcionalidades deste *software* utilizado no capítulo 3 "Determinação de áreas prioritárias para prospecção de fósseis de herbívoros da megafauna Quaternária".